THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

May 15, 1970 Paper 47

SIGNIFICANCE OF SUTURES IN PHYLOGENY OF AMMONOIDEA

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ABSTRACT

Because of their complex structure ammonoid sutures offer best possibilities for the recognition of homologies. Sutures comprise a set of individual elements, which may be changed during the course of ontogeny and phylogeny as a result of heterotopy, heteromorphy, and heterochrony.

By means of a morphogenetic symbol terminology, sutural formulas may be established which show the composition of adult sutures as well as their ontogenetic development. WEDEKIND's terminology system is preferred because it is the oldest and morphogenetically the most consequent, whereas RUZHENTSEV's system seems to be inadequate because of its usage of different symbols for homologous elements. WEDEKIND's system includes only five symbols: *E* (for external lobe), *L* (for lateral lobe), *I* (for internal lobe), *A* (for adventitious lobe), *U* (for umbilical lobe).

Investigations on ontogenetic development show that all taxonomic groups of the entire superorder Ammonoidea can be compared one with another by means of their sutural development, expressed by their sutural formulas. Most of the higher and many of the lower taxa can be solely characterized and arranged in phylogenetic relationship by use of their sutural formulas.

INTRODUCTION

Today very few ammonoid workers doubt the importance of sutures as indication of ammonoid phylogeny. The considerable advances in our knowledge of ammonoid evolution during recent decades have been based overwhelmingly upon investigations of sutures.

In general, recognition of homologies is regarded as the principal method of phylogenetics. Recognition of homologous similarities, and differentiation of homologous from analogous structures of similar function, are the prime indicators of the relationships of organisms.

Among ammonoids sutures offer best possibilities for the identification of homologies, for they are manifestations of highly complex anatomical structures, and the linear nature of sutures allows comparisons between them to be made with relative ease. Other characteristics (e.g., conch shape, sculpture, growth lines) represent less complicated structures; therefore, numerous homeomorphs restrict the usefulness of these features for phylogenetic investigations.

The exact function of the specific form of the septum and its correlation with organs of the ammonoid animal are not yet known. At any moment in the life of the animal the intimate relationship between the last septum and soft parts of the organism is shown by the morphological positions of this septum, which forms the adapical termination of the body-chamber against the phragmocone. Because the septum is so much a part of the general organization of the ammonoid animal, changes in soft parts connected to the septum are always accompanied by changes in the septum. Important changes of the suture during ontogeny and in the phylogeny of any

ammonoid group thus reflect changes of the other organs of the ammonoid animal.

The great overall stability and phylogenetic irreversibility of suture development strongly imply an extensive system of pleiotropic genes and polygenic characters (see KOSSWIG, 1959, p. 218). This indicates that the suture represents a large amount of the genetic material of the organism. From the genetical point of view, then, importance of the suture in ammonoid phylogeny and systematics is obvious.

The recognition of homologous structures in the suture is based upon two kinds of information —stratigraphic succession of the ammonoids and their ontogenetic development. The first depends upon favorable stratigraphic sections, and the second upon favorable preservation of the fossils.

The methodological prerequisites for recognition of homologies and their role in the identification of phylogenetic relationships were treated in a precise way by REMANE (1952). Also, application of homology criteria to ammonoid sutures has been discussed by SCHINDEWOLF in numerous publications (e.g., 1961-69).

Lobes are individual elements of the suture. In ontogeny they are formed first after conclusion of the larval stage (i.e., after formation of the prosuture). Individual lobes are designated in accordance with their original position relative to other elements. During ontogeny and phylogeny three types of changes can occur: the position of lobes may change (heterotopy); the lobe itself may change (heteromorphy); or the ontogenetic time of appearance of a lobe may change (heterochrony).

In the course of ontogeny individual elements may be reduced as, for example, in *Spiroceras bifurcati* (QUENSTEDT) as reported by SCHINDEWOLF (1951, p. 29, fig. 17; 1961, p. 92, fig. 45). Disappearance of elements during ontogeny, as for example in *Paracuariceras incisum* (see SCHINDEWOLF, 1965, p. 496, fig. 296) and perhaps *Agathiceras uralicum* KARPINSKY (see MILLER & FURNISH, 1957, p. *L*23, fig. 11; RUZHENTSEV, 1956, fig. 29) seems to be rare. In the course of phylogeny, however, simplification of sutures is not at all uncommon as, for example, in the clymeniids where forms with few sutural elements are derived from others with many lobes; also certain Cretacous ammonoid taxa with quadrilobate primary sutures stem from forms with five-lobed primary sutures.

Morphological features observed in the ontogenetic development of sutures in numerous ammonoid genera, together with symbols adopted for such parts as their lobes and saddles, are illustrated in Figures 1 to 10, inclusive, distributed through most of the discussions given in the present paper. Summaries of suture development contained in Figures 11 to 16 follow other illustrations in a group toward the end of the paper. Such an arrangement should be most convenient for readers and it is hoped will facilitate their understanding. Attention may be called here to the editorial practice of printing symbols for suture parts in italics throughout the text, for it is judged that simplicity and clarity are furthered by this typographic distinction. Lettering on diagrams speaks for itself.

ACKNOWLEDGMENTS

We wish to thank Professor O. H. SCHINDEWOLF for his active interest and helpful discussions. Appreciation is extended to Professors R. C. MOORE and CURT TEICHERT, Lawrence, Kansas, for critical reading of the manuscript and offering many valuable suggestions. J. KULLMANN is responsible for the introductory part, explanation of WEDEKIND's terminology and discussion of Paleozoic ammonoids; he expresses his thanks to Dr. R. A. DAVIS, formerly Iowa City, Iowa, and now at Swansea, Wales, for stimulating discussion of the introductory parts of the present work. J. WIEDMANN is responsible for the discussion of Mesozoic ammonoids.

DESIGNATION OF INDIVIDUAL PARTS OF SUTURES

For purpose of communication among paleontologists a terminology for individual elements of complex ammonoid sutures is necessary. Two types of terminology, not necessarily mutually exclusive, have been used: a morphographic-descriptive system and one based on morphogenesis. The former, based on position of individual elements in the adult suture is by far simpler and serves well for communication of morphological data. The latter, based on ontogenetic development, seems to be more useful in communicating information about homologies. When a strictly morphogenetic suture terminology is used, each element of the mature suture is

designated by a symbol which records the entire ontogeny of that element. Such symbols can be gathered together into groups which record the ontogeny of the adult suture. These groupings of symbols have been called sutural formulas.

It is possible to symbolize each element of the adult ammonoid suture solely by its position in the suture. Such symbols can be grouped into what resembles the sutural formula as described above but indicates only the relative position of the sutural elements in the adult suture.

NOETLING (1905, 1906) first used a morphogenetic symbol terminology. WEDEKIND (1913) improved this and later applied his system to ammonoids in general. His is the oldest practicable morphogenetic system of terminology.

SCHMIDT (1921) added morphographical symbols to the morphogenetical terminology of WEDEKIND. RUZHENTSEV (e.g., 1949, 1957), using what is essentially WEDEKIND's system, proposed a number of new names and symbols for sutural elements and his lead has been followed by several American authors (e.g., FURNISH, GLENISTER, MCCALEB, NASSICHUK). Soviet colleagues (notably POPOV, 1965) have made additional terminological modifications.

WEDEKIND'S TERMINOLOGY

WEDEKIND's terminology was applied primarily to the primary suture, which is the second suture to be formed. The so-called prosuture, which precedes the primary suture, belongs to the proseptum and is part of the protoconch. The first-formed suture shows in earliest ammonoids a simple circle, in later representatives a prominent external saddle, thus differing basically from all following sutures. The majority of all Paleozoic ammonoids have a primary suture with three lobes ("protolobes"), for which three symbols are required and two more for lobes ("metalobes") which arise from the two saddles of the primary suture. Should several lobes originate in succession in the same place, then the symbols are designated by numbers according to their order of origin. In this way we can describe the ontogenetic development of the suture from the primary suture to the last septum quite adequately, using five symbols only.

The simple procedure stated can become complicated by the subdivision of single lobes, if these divisions become independent lobes. If the newly formed part-lobes or whole lobes are clearly separated by saddles, they can be designated according to their position by supplementary letters *v* (ventral), *m* (medial), and *d* (dorsal) (e.g., $E_1 \rightarrow E_{1v}E_{1m}E_{1d}$). Single lobes formed in this way may be subdivided repeatedly (e.g., $E_{1d} \rightarrow E_{1dv}E_{1dm}E_{1d2}$; $E_{1d2} \rightarrow E_{1d2v}E_{1d2m}E_{1d3}$—with understanding that the latter numeral in E_{1d2}, E_{1d2v}, E_{1d3}, etc., indicates the quantity of the preceding letter). On the other hand, if a lobe divides into a series of incisions (e.g., *Crimites*, $U_4=S$, Fig. 12,*e*), it is designated by the letter *S* (*Suturallobus*, WEDEKIND, 1916; SCHINDEWOLF, 1961, p. 63-78, fig. 31). Since the incisions do not represent homologous units, their detailed notation is superfluous. A morphological description of the incisions would unnecessarily complicate formula characterization of the sutures, and any gain would be small, as such sutural characteristics are neither generic, nor even specific, peculiarities, and often occur asymmetrically.

Brackets and colons, introduced by RUZHENTSEV, serve to classify parts of the suture. Lobes in the process of division are placed in brackets so long as their intermediary saddles have not reached the height of the neighboring saddles. It is difficult to decide at what point a lobe in the process of development becomes independent, however. A colon is used to represent an umbilical seam and can be used with adequate accuracy only when a saddle lies on an umbilical seam. If a lobe is halved by the umbilical seam the use of a colon becomes meaningless. Successive stages in sutural development are indicated by arrows between sutural formulas or corresponding parts of suture formulas.

In the order of their phylogenetic appearance the five symbols proposed by WEDEKIND are:

E (Externlobus), external lobe; abdominal lobe *sensu* HYATT (1867) (synonyms: *V*=ventral lobe, RUZHENTSEV, 1949, *M*=median lobe, WEDEKIND, 1913, which signified the medial parts of a bipartite external lobe). This is the first lobe, already found in bactritids and almost all ammonoids, which appears in the vicinity of the siphuncle, and only in a few groups (Clymeniida, Pseudohaloritidae) does it lose its spatial connection with the latter. The external lobe is cut by the median plane and lies on the outer side of the spiral shell, spanning the space between the two external saddles. Loss of the external lobe is restricted to the clymeniids.

L, lateral lobe (synonyms: *G*=*Brückenlobus*, SCHMIDT, 1921; *P*=pleural lobe, SCHMIDT, 1952;

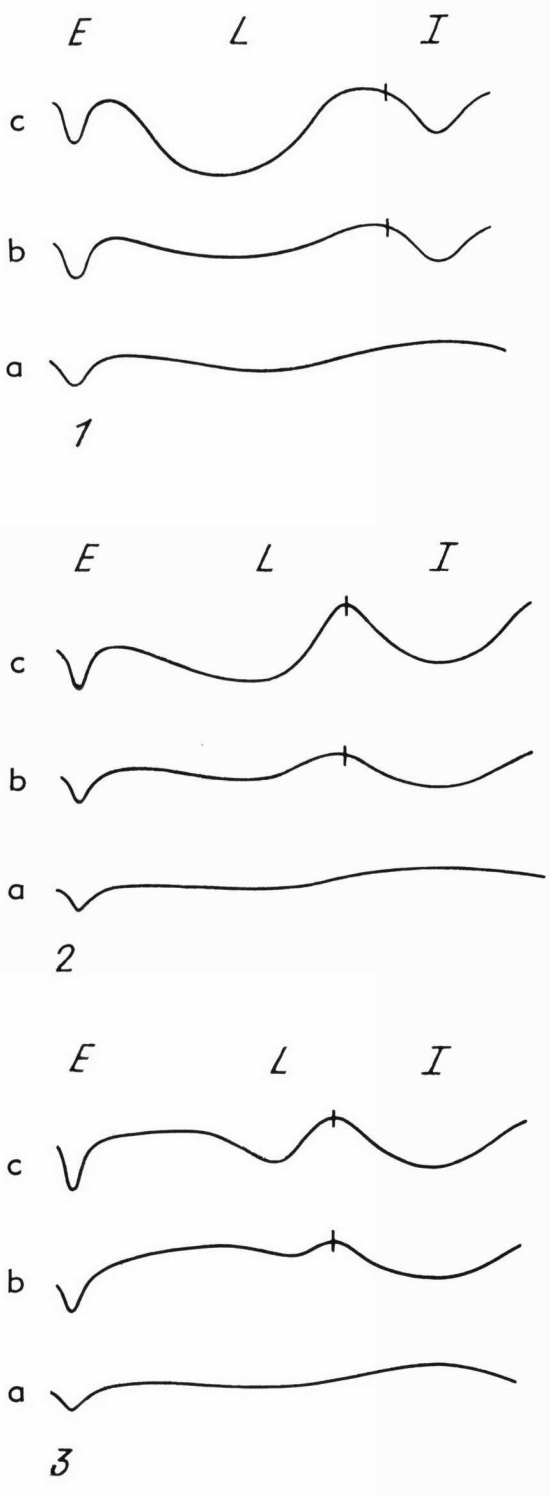

FIG. 1. Ontogenetic development of sutures in genera of Anarcestina (Goniatitida).——*1. Mimagoniatites zorgensis* (ROEMER), Lower Devonian (upper Emsian), Germany.——*2. Latanarcestes noeggerati* (VON BUCH), Middle Devonian (Eifelian), Germany.——*3. Anarcestes lateseptatus* (BEYRICH), Middle Devonian (Eifelian), Germany. (All after Schindewolf, 1933, fig. 19, 25, 26; sutures drawn to same length).

[The sutural development of *Latanarcestes* presents an intermediate stage between those of *Mimagoniatites* and *Anarcestes*. The lateral lobe of *Latanarcestes* is located laterally like that of *Mimagoniatites* whereas the corresponding lobe of *Anarcestes* lies more on the flank close to the umbilical seam. In RUZHENTSEV's terminology, the lateral lobe of *Mimagoniatites* is indicated by the symbol *O*, and those of *Latanarcestes* and *Anarcestes* by *U*.]

O=omnilateral lobe, RUZHENTSEV, 1957; *ex parte: U*=umbilical lobe *sensu* RUZHENTSEV, 1949, not U^1, U^2, etc. *sensu* RUZHENTSEV; not *L*=lateral lobe *sensu* RUZHENTSEV, 1949). The second lobe to appear in the history of the ammonoids is similarly present in some bactritids and practically all ammonoids. In forms where the suture consists of *E* and *L* the latter is broad and occupies the area between the external and internal saddles. A narrowing of the lateral lobe is already perceivable in Early Devonian forms, and this comes about either as result of introduction of a broad internal lobe with wide saddles between *I* and *L* (e.g., *Mimosphinctes*), or as result of expansion of the external saddle and increase in involution with slow corresponding increase in the height of the whorls (e.g., *Anarcestes,* with *Latanarcestes* as a transition, see Fig. 1). RUZHENTSEV opposed this view and in his opinion the lobe is, in the first case, the omnilateral lobe and, in the second case, the umbilical lobe. However, we believe that no morphogenetic foundation supports this view.

I, internal lobe (synonyms: *D*=dorsal lobe, RUZHENTSEV, 1949; not *I*=internal lateral lobe *sensu* RUZHENTSEV, 1949). The third lobe in phylogenetic order of appearance is that cut by the median plane and which lies in the inner zone of the whorl. We encounter *I* for the first time in advolute coiled forms (*Mimosphinctes cantabricus* KULLMANN); in some it is replaced by a later internal saddle. The following two symbols introduced by WIEDMANN (1966b), represent special cases of *I* and occur mainly in Mesozoic forms: I_l=lituid *I*, a simple, unfrilled, double-pointed internal lobe (restricted to Phylloceratida); I_s=septal lobe, bifid extension of the internal lobe climbing up the face of the preceding septum (restricted to Lytoceratina).

The two lobes described next are those which originate through division of saddles.

U (Umschlaglobus), umbilical lobe, WEDEKIND (1913) (synonyms: *K=Kehllobus,* SCHMIDT, 1921, and *U=Umschlaglobus sensu* SCHMIDT, 1921; *I*=internal lateral lobe *sensu* RUZHENTSEV, 1949, and U^1, U^2, etc., *sensu* RUZHENTSEV, 1949; not *U*=umbilical lobe without superscript *sensu* RUZHENTSEV, 1949). A lobe (or series of lobes) which originates from the saddle area between internal and lateral lobes, and which then occurs in the vicinity of the umbilicus either on the outer or inner part of the shell is defined as the umbilical lobe. The development of umbilical lobes pushes the lateral lobe from its umbilical position out onto flanks of the shell, provided that no adventitious lobes are formed. All Mesozoic ammonoids possess at least one umbilical lobe in their primary suture. In the course of their ontogeny a small number of Mesozoic ammonoids develop one or more lobes on the saddle between U_1 and *I*. Since these originate in the umbilical area they are designated U_n.

SCHMIDT and RUZHENTSEV have related the umbilical lobe to shell morphology. SCHMIDT differentiated between lobes which originate from the internal saddle and develop externally *(U)* or internally *(K)*. The latter can shift to the flanks of the shell during ontogeny. RUZHENTSEV renamed WEDEKIND's *L* as *U*, but distinguished between U_1 *sensu* WEDEKIND which he called *I*, which always lies internally, and all other umbilical lobes. The sequence of origin continues in RUZHENTSEV's terminology with U^1, U^2, etc., but in some cases with I^1, I^2, etc. WEDEKIND's terminology is advantageous in that the lobal sequence can be expressed clearly in a formula. For example, RUZHENTSEV expressed the formula of *Protocanites* as: VUU^1ID, whereas WEDEKIND's formula is ELU_2U_1I. The latter formula makes it possible to read off [RUZHENTSEV's symbols in parentheses] that $U_1(I)$ is developed before $U_2(U_1)$. The difference is even more noticeable in the case of some Mesozoic ammonoids. RUZHENTSEV described the suture of *Normannites* sp. as follows:

$(V_1V_1)\ \ (U_2U_1U_2)\ \ U^1I_2I^2{}_1I^3{}_1 : I^3{}_1I^2{}_1I^1{}_1I^1D,$

whereas WEDEKIND's formula is:

$$ELU_2U_3U_5 : U_1U_1U_nI.$$

In this case the latter is not only shorter and clearer but contains more information.

A, adventitious lobe *(Adventivlobus),* WEDEKIND, 1916 (synonyms: *L*=lateral lobe *sensu* RUZHENTSEV, 1949; *N*=neolateral lobe, POPOV, 1965). A lobe (or series of lobes) which develops from the external saddle. The formation of adventitious lobes pushes the lateral lobe back into an umbilical position, provided that no further umbilical lobes are developed.

COMPARISON OF TERMINOLOGIES USED BY WEDEKIND AND RUZHENTSEV

RUZHENTSEV's declared aim, in contrast to that of SCHMIDT, is a morphogenetical terminology. In some respects, however, RUZHENTSEV provided a morphographic-descriptive terminology, a fact that is evident only after careful analysis of his system (see SCHINDEWOLF, 1968, p. 835ff.). Unfortunately, scrutiny of RUZHENTSEV's viewpoint is made more difficult because of the polemics in his works (especially 1960, 1964). In the following we shall only touch upon some more important points in dealing with the controversy between WEDEKIND and RUZHENTSEV.

RUZHENTSEV's bias toward a descriptive viewpoint of sutures is evident from the importance attached by him to the mere names of symbols. He substantiated his use of the symbols *L, U,* and *I* (of WEDEKIND) in a different context in that the symbols chosen by WEDEKIND are much better suited for other lobes. In doing so RUZHENTSEV failed to perceive that the importance of names from which the symbols are derived is irrelevant in a nomenclature based on morphogenetical symbols. Quite the opposite is the case as we assume, from the outset, that the individual elements will change their position and shape in the course of ontogeny. For example, it is not significant whether a lobe is called dorsal, external, or ventral. What is decisive is which part of the adult suture can be traced back to the *E* lobe of the primary suture. From a comparison of *E* in various forms we can work out its ability to change in the course of ontogeny and phylogeny, which, in turn, is important for the systematics and phylogeny of the form in question.

The principle of comparison of homologous structures in ammonite sutures was developed by NOETLING and WEDEKIND half a century ago. The nomenclature is that of WEDEKIND. RUZHENTSEV opposed this terminology, arguing that the main three designations were incorrectly used:

1) external lobe instead of "ventral lobe"; 2) internal lobe in place of "dorsal lobe," and 3) lateral lobe for "umbilical lobe" and "omnilateral lobe." In addition to what has already been said, that the name is unimportant for the meaning of a symbol, the following pertinent objections to RUZHENTSEV's opinions may be raised:

1) The terms internal and external are unrelated to the orientation of the ammonite animal, whereas the terms dorsal and ventral, when applied to position of the last septum, can refer to various parts of the septum depending on length of the body chamber. For this reason HYATT (1867) proposed the name "abdominal lobe" for the external lobe. Having regard to MUTVEI's opinions regarding the orientation of *Nautilus* a renaming of *V* and *D* as anterior and posterior lobe ought to be considered.

2) As to the lateral lobe, RUZHENTSEV advocated that the lobe defined by WEDEKIND as lying between internal and external lobes, called lateral by him, is, in fact, an umbilical lobe *(U)* when it is small and situated near the umbilicus, or an omnilateral lobe *(O)* when it is broad and occupies the entire lateral side. As RUZHENTSEV expressly stated, *O* is later replaced by *U*, which means that they are homologous (see Fig. 1). Conversely, *U* can develop into *O*, as in *Foordites, Pinacites,* and other genera (see SCHINDEWOLF, 1968, p. 841, fig. 474—477). This demonstrates that the "omnilateral lobe" and the "umbilical lobe" *sensu* RUZHENTSEV represent homologous, heteromorph variations of the same lobe. A renaming of *L* as *O* and *U* is therefore not justified.

3) The priority of WEDEKIND's symbols is indisputable, because in a morphogenetic terminology, as stated above, it can only be a question of *symbols,* since these represent homologous units. The appropriateness of a name does not affect its priority: chemical symbols are not altered when the name of a substance is found to be inappropriate. For example, in the case of "Oxygenium"=*O*, contrary to LAVOISIER, not all acids contain oxygen. RUZHENTSEV's objection that SCHINDEWOLF ignored the rules of priority in respect of *U* is unfounded. WEDEKIND derived the symbol *U* from the word *Umschlaglobus;* SCHINDEWOLF later correctly latinized the German word for the sake of international clarity *(Umbilikallobus)*. In so doing he did not alter the symbol. All in all, it follows that RUZHENTSEV's renaming is in no way "a new type of nomenclature which is substantially different from the former one" (RUZHENTSEV, 1962, p. 271), but rather a retrogression to earlier descriptive designations. Superfluous and homologous terms contribute to disorder rather than aid in clarifying the modes of development of sutures. Future research in the field of computer-calculation of septal-area composition will be considerably handicapped by such terms.

In the following use is made of WEDEKIND's terminology, because it is the older and, in our opinion, the more logical system. In the interests of simplicity in scientific work the use of various symbols for one and the same object should be avoided. Since, however, the younger terminology of RUZHENTSEV has been used in some important publications a conversion table of WEDEKIND's, RUZHENTSEV's, and POPOV's symbols is here included (Table 1).

TABLE 1. *Comparison of some ammonoid suture-symbol terminologies.*

[SCHMIDT's terminology is not included because it is specifically morphographic.]

WEDEKIND	RUZHENTSEV	POPOV
E (E_1)	V	V
E_2, E_3, . . .	V^1, V^2, . . .	
L	O *or* U *(not* U^1, U^2, . . .*)*	L
I	D	D
I_1	(D_1D_1)	
I_s	D	
A (A_1)	L	N
A_2, A_3, . . .	L^1, L^2, . . .	
U (U_1)	I	K
U_2, U_3, . . .	U^1, U^2, . . .	
U_n	I^1 *(rarely:* I^2 *or following)*	

SUTURAL DEVELOPMENT IN LARGER SYSTEMATIC UNITS

PALEOZOIC AMMONOIDS

ORDER GONIATITIDA

The starting point of sutural development in the superorder Ammonoidea is a suture characterized by the elements *ELI,* which can be found in the adult mature suture of forms of the superfamily Anarcestaceae (order Goniatitida, suborder Anarcestina). These occur typically in the upper part of the Lower Devonian. The most primitive Lower Devonian genera exhibit *EL,* whereas the advanced Middle Devonian forms have the four elements *ELUI. Maenioceras* (upper Givetian) has the most complicated suture $EALU_2U_1I$ (Fig. 11,*a*) and in contrast to the tornoceratids only *L* is on the flank of the whorl, since U_1 (and U_2?)

are formed before *A*. In a side branch (*Augurites,* Fig. 11,*b*) the external lobe appears to be split up into $E_1E_2E_mE_2E_1$. On the basis of their sutures RUZHENTSEV considered the Agoniatitidae (+ Mimoceratidae) and Anarcestidae to be separate suborders. In his terminology the Agoniatitina have an "omnilateral lobe" and the Anarcestina an "umbilical lobe." The sole difference between *"O"* and *"U"* is that the questionable lobe *L* in *Anarcestes* and younger members of the family lies near the umbilicus, in contrast to the Agoniatitidae (Fig. 1). The oldest anarcestids are intermediary forms where, in all stages (as in *Mimagoniatites*) *L* is broadly developed on the whorl flank. In younger anarcestids *L* is restricted by the external saddle so that, combined with the greater involution of the shell, *L* lies in most Anarcestidae near the umbilicus. Therefore, evidently no genetic difference distinguishes *"O"* from *"U" sensu* RUZHENTSEV.

The superfamily Pharciceratacea also belongs to the suborder Anarcestina, its characteristic difference from the Anarcestaceae being the development of a median saddle and lobe in the external lobe. The basic sutural pattern is $(E_1E_mE_1)LI$, as in *Ponticeras*. Within both of the Gephuroceratidae and Pharciceratidae one or more umbilical lobes occur: *Manticoceras* $(E_1E_mE_1)L{:}UI$ (Fig. 11,*c*); *Timanites:* $(E_1E_mE_1)LU_2U_3{:}U_1I$; *Pharciceras:* $(E_1E_mE_1)LU_2U_4{:}U_3U_1I$; *Synpharciceras:* $E_mE_1LU_2U_4U_6U_8U_{10}{:}U_9U_7U_5U_3U_1I$; *Neopharciceras* up to U_{24}. In the family Beloceratidae there is, in addition, a marked division of the external lobe: $E_xE_mE_xLU_yI$ (e.g., *Mesobeloceras:*

$$E_mE_3E_2E_1LU_2U_3U_5U_7{:}U_8U_6U_4U_1I$$

(Fig. 11,*d*), *Beloceras* up to E_7 and U_{18}). The use of formulas in these cases is somewhat restricted owing to asymmetry and irregular bifurcation of the suture.

The Prolobitaceae represent the third superfamily of the suborder Anarcestina. Their suture appears to be made up of *ELI* and $ELU_1(I_1I_1)$ (Fig. 11,*e*); however, the group is poorly known.

In the Anarcestina lobal increase usually takes place in the umbilical area, if not also in the area of the external lobe. The suborder Goniatitina, however, is characterized by the appearance of a first adventitious lobe *(A)* prior to formation of an umbilical lobe *(U)*. This means that the lateral lobe remains in the umbilical area (Fig. 2). The simplest sutural formula is, therefore, *EALI (Tornoceras, Cheiloceras)*. The following lobal ontogeny is valid for all later members of the suborder: Primary suture *ELI*, then (usually 2nd suture) *EALI*, and later *EALUI*. The formula *EALUI* occurs most commonly within the superfamily Cheiloceratacea (including Tornoceratidae and Pseudohaloritidae), i.e., the most primitive Goniatitina. An increase in the number of elements follows from an increase in the adventitious lobes (e.g., *Discoclymenia:* $EA_3A_2A_1L{:}UI$), (Fig. 11,*f*).

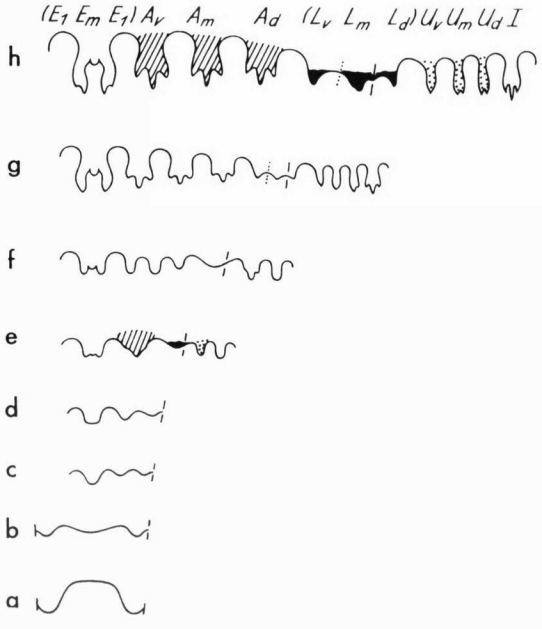

FIG. 2. Ontogenetic development of suture in *Marathonites (Almites) invariabilis* RUZHENTSEV, Lower Permian (lower Artinskian), USSR (southern Urals). (After Ruzhentsev, 1956, fig. 89a-f, i, 1). [Explanation: *a,* prosuture; *b,* primary suture; *c,* 2nd suture; *d-g,* intermediate-stage sutures; *h,* adult suture. The primary suture is trilobate; the 2nd suture has an adventitious lobe that during ontogeny, like the umbilical lobe, divides into 3 lobes.]

Other superfamilies differ from the Cheiloceratacea principally in that the external lobe has a median saddle and lobe. Their sutural formula is $(E_1E_mE_1)ALUI$ (Fig. 11,*g*). The superfamily Goniatitaceae has the basic suture from which sutures of other Goniatitina superfamilies differentiate. By and large, the families Goniatitidae, Gastrioceratidae, and Paragastrioceratidae retain the formula $(E_1E_mE_1)ALUI$. A few families (Metalegoceratidae and Schistoceratidae) show a tendency toward trifid division of some lobes. This is typical of the superfamilies Agathiceratacea and Cyclolobaceae. The Metalegoceratidae

subdivide the lateral lobe *L* into $L_vL_mL_d$ (Fig. 11,*h*) [the end form being *Pseudoschistoceras* $(E_1E_mE_1)AL_v$ $(L_{mv}L_m{:}L_{md})L_dU_1I$ (Fig. 11,*i*) according to RUZHENTSEV, 1962]. The Schistoceratidae subdivide U_2 into $U_{2v}U_{2m}U_{2d}$ (end form *Schistoceras* $E_mE_1ALU_{2v}U_{2m}{:}U_{2d}U_1I$).

The Agathiceratacеae similarly exhibit a tendency toward trifurcation, in this case of the adventitious lobe and partly of the external lobe: 1) the Delepinoceratidae display incipient trifurcation of E_1 and *A* [*Delepinoceras* $(E_{1d}E_{1m}E_{1v}E_mE_{1v}E_{1m}E_{1d})(A_vA_mA_d)L{:}UI$] (Fig. 11,*k*); 2) in the Agathiceratidae only *A* trifurcates [*Proshumardites* $(E_1E_mE_1)(A_vA_mA_d)LUI$; the end form is *Agathiceras* $(E_1E_mE_1)A_vA_mA_dLUI$] (Fig. 12,*a*).

The superfamily Cyclolobaceae is characterized by trifurcation of all lobes except *E*. Examples of the family Shumarditidae are *Shumardites* $[E_mE_1A_vA_mA_dL : (U_vU_mU_d)\,(I_1I_mI_1)]$ and *Properrinites* $[(E_1E_mE_1)A_vA_m(A_{dv}A_{d2})\;\; L_vL_m : L_d\;\; (U_{v2}U_{vd})U_mU_d(I_1I_mI_1)]$.

The same scheme of lobal development prevails in the families Marathonitidae and Cyclolobidae. Lobal multiplication results from repeated trifurcation of *A* and *U*, while the lateral lobe remains single trifid. Examples of the family Cyclolobidae are *Vidrioceras* $[(E_1E_mE_1)\,A_vA_mA_dL_vL_mL_d{:}U_vU_mU_d\,(I_1I_mI_1)]$, *Stacheoceras*

$$[(E_1E_mE_1)A_vA_mA_{dv}A_{d2v}A_{d3v}A_{d4v}\,(A_{d5v}A_{d6})L_vL_mL_d{:}U_{v4}U_{v3d}U_{v2d}U_{vd}U_mU_d\,(I_1I_mI_1)],$$

and *Waagenoceras*

$$[(E_1E_mE_1)A_vA_mA_{dv}A_{d2v}A_{d3v}A_{d4v}(A_{d5v}A_{d6})\;\; L_vL_m{:}L_dU_{v3}U_{v2d}U_{vd}U_mU_d(I_1I_mI_1)].$$

The family Popanoceratidae is basically similar except for the insertion of further adventitious and umbilical lobes as in *Popanoceras*

$$(E_1E_mE_1)A_{1v}A_{1m}A_{1dv}(A_{1d2v}A_{1d3})A_2LU_2{:}\;\; U_3(U_{1v2}U_{1vd})U_{1m}U_{1d}(I_1I_mI_1)$$

(Fig. 12,*b*); in *P. sobolewskyanum, teste* RUZHENTSEV (1956), the sequence U_2 and U_3 cannot be verified with certainty. These similarities are of special importance for the systematics of these three families as they prove their relationship to one another.

In the superfamily Dimorphoceratacеae we find a totally different lobal configuration. The family Neodimorphoceratidae is similar at first to the family Goniatitidae, but differs in that the number of lobes of its suture increases through differentiation of the external lobe. The end form is *Neodimorphoceras* $(E_1E_2E_mE_2E_1)AL{:}UI$ (Fig. 12,*d*). The family Thalassoceratidae has no additional lobal elements. In contrast the family Dimorphoceratidae often exhibits irregular subdivisions of the external lobe and on occasion also of the adventitious lobe. Examples are *Asturoceras* $(E_{1d}E_{1vd}E_{1v2}E_mE_{1v2}E_{1vd}E_{1d})AL{:}UI$ (Fig. 12,*c*) and *Paradimorphoceras*

$$(E_{1d}E_{1v}E_mE_{1v}E_{1d})(A_vA_d)L{:}UI.$$

The superfamily Adrianitaceae, in form and lobal arrangement very similar to the Agathiceratacеae, increases its lobes by the formation of additional umbilical lobes. Characteristic of many Adrianitaceae is the breaking down of a lobe in the region of the umbilicus into numerous incisions, to which we can give no names. This is referred to as *Suturallobus (S)* by WEDEKIND. Examples are *Emilites* $(E_1E_mE_1)AL(U_2{=}S)U_1I$ and *Crimites* $(E_1E_mE_1)ALU_3(U_4{=}S)U_2U_1I$ (Fig. 12,*e*).

In RUZHENTSEV's terminology *Suturalloben (S)*, which are lobes appearing simultaneously, are given identical symbols [e.g., *Crimites* $(V_1V_1)LUU^3U^4U^4{:}U^2U^1ID$]. This means, in the cited example, that U^4 represents two different lobes. This method of notation breaks down in complicated forms where differences can occur within a species or even in an individual in one particular asymmetrical septum (see RUZHENTSEV, 1956, fig. 94-95). Such irregularities are evidence of abnormal lobal increase and are expressed best by use of the additional symbol *(S)*, used in conjunction with the usual lobe symbol.

The oldest forms of the suborder Prolecanitina are similar to the Cheiloceratidae. The suture of *Protocanites* possesses the same number of elements as that of the contemporaneous *Gattendorfia*. The origin of their five lobes is different, however: in *Gattendorfia* $EALUI$ and in *Protocanites* ELU_2U_1I. It is by no means certain that lobal increase occurs uniformly in the entire suborder through insertion of umbilical lobes. SCHINDEWOLF (1951, p. 22, fig. 14) reported the presence of an adventitious lobe in *Neopronorites permicus*—an interpretation which cannot be proved, since the trilobate primary suture in this form is immediately followed by a quinquelobate suture. The absence of an adventitious lobe has been demonstrated clearly for *Merocanites asiaticus* (KARPINSKY) which has the sutural formula $ELU_2U_3{:}U_1I$ (Fig. 3), but the possibility exists that the lobe taken to be *L* in other Prolecanitina is in fact the lobe *A*.

The basic family Prolecanitidae shows an in-

crease in *U* from *Prolecanites* $[(ELU_2U_3U_4{:}U_1I)$ (Fig. 12,*f*)] up to U_7 in *Acrocanites*. In the Daraelitidae and Pronoritidae the number of umbilical lobes is increased even more and, in addition, *E* is further developed in *Daraelites* $[(E_1E_mE_1)LU_2U_3U_4U_5 \ldots U_6U_1(I_1I_1)$ up to $U_9]$ and *Neopronorites* $[(E_1E_mE_1)(L_vL_d)U_2U_3U_4 \ldots U_5U_1(I_1I_1)$, up to $U_{10}]$.

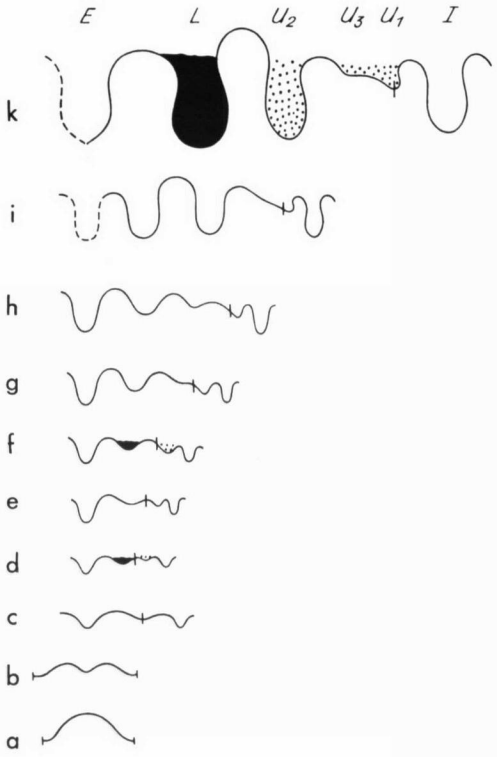

FIG. 3. Ontogenetic development of the suture in *Merocanites asiaticus* (KARPINSKIY), Lower Carboniferous (lower Visean), USSR (from Karpinskiy, 1896, p. 187). The primary suture is trilobate; later on a 4th lobe is developed (umbilical lobe), which pushes the lateral lobe from its original umbilical position out onto the flanks. [*a*, prosuture; *b*, primary suture; *c-i*, further stages of development; *k*, adult suture.]

The superfamily Medlicottiaceae retains the sutural development of the Prolecanitaceae with modification of the external saddle in that parts of the lateral lobe lying near the external lobe become included in the external saddle. The incisions which result cannot be traced morphogenetically and commonly are not generically, or even specifically, typical. Furthermore, they may be asymmetrical. RUZHENTSEV's notation, therefore, would appear to be superfluous. Examples are *Prouddenites* $[(E_1E_mE_1)(L_{v2}L_{vd}L_d)U_2U_3U_4U_5 \ldots U_6U_1(I_1I_1)$ (Fig. 12,*g*)], *Uddenites* $[(E_1E_mE_1)(-L_d)U_2U_3U_4U_5U_7 \ldots]$, and *Medlicottia* $[(E_1E_mE_1)(-L_d)U_2U_3U_4U_5U_7 \ldots]$.

The superfamily Sageceratacea is characterized by elaboration of the external lobe, as in *Pseudosageceras* $[E_mE_4E_3E_2E_1LU_2U_3U_4U_6 \ldots U_5U_1(I_1I_1)$ (Fig. 12,*h*)] (see BOGOSLOVSKIY *et al.*, 1962).

The lobal development of some isolated groups systematically close to *Praeglyphioceras, Karagandoceras,* and *Prodromites* remains unexplained. In these a median lobe develops in the external saddle $(E_1E_mE_1)$. The first two genera belong in the suborder Goniatitina, since the lobe lying laterally appears to be adventitious. The suture of *Prodromites,* on the other hand, has the formula $E_mE_1LU_2U_3 \ldots$ and, therefore, probably belongs in the suborder Prolecanitina. It is possible that these are independent, restricted groups which existed for a short time and left no successors.

ORDER CLYMENIIDA

Members of the order Clymeniida are restricted to the uppermost Devonian and are close to the Anarcestina. The sutural formula *ELI* occurs here, too, and further, as in the Anarcestina, lobal increase occurs primarily in the umbilical lobe and secondarily in the adventitious lobe.

The greatest similarities with the Anarcestina are found in the suborder Gonioclymeniina. Lobal development proceeds from *ELI* via *ELUI* and *EALUI* to $EA_2A_1LU_1U_2I$ *(Sphenoclymenia)* (Fig. 12,*i*). Some families develop a median saddle in the external lobe (e.g., *Biloclymenia*) $(E_1E_mE_1)LU_2U_1I$. Among the Parawocklumeriaceae a lobal reduction occurs from $(E_1E_1)L{:}(I_1I_1)$ to a single *L*.

The suborder Clymeniina includes the typical clymeniids where the external lobe is reduced in the adult stage. The basic suture is *L:I*, and advanced forms have either *ALI* or *LUI*. *Cymaclymenia (AL/UI)* (Fig. 12,*k*) is the most complicated genus of the suborder.

MESOZOIC AMMONOIDS

Viewed broadly, Mesozoic ammonoids are characterized by a progressive development of the suture. This involves both denticulation of the adult suture and number of lobes in the primary suture. The first, as is well known, proceeds from the unipolar *"ceratitic"* frilling of the lobes of most Triassic ammonites to the bipolar *"am-*

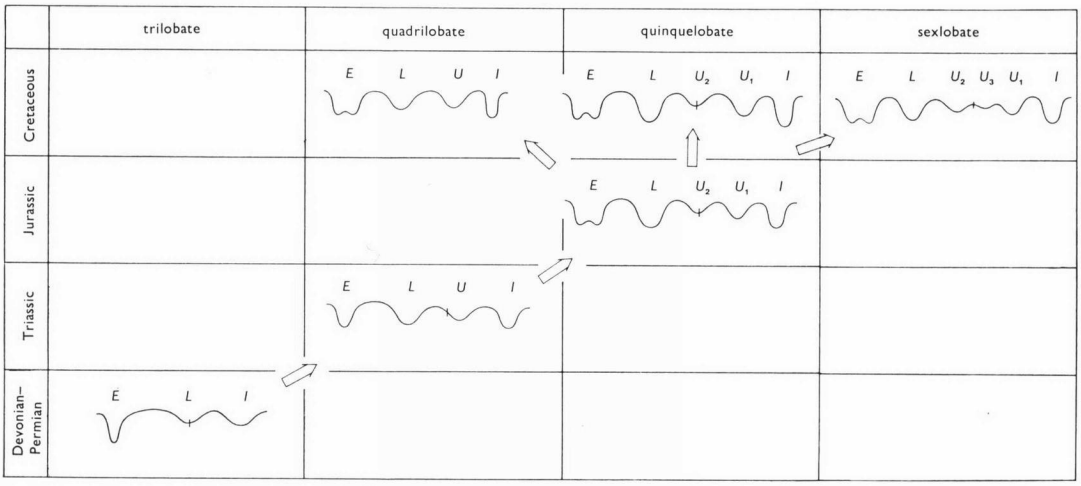

FIG. 4. Progressive and regressive evolution of primary sutures in ammonoids.

monitic" frilling of the lobes and saddles of Jurassic and Cretaceous ammonites. The primary suture (Fig. 4) of the Triassic ammonites has gained an extra element over its Paleozoic forerunners, and thus has become ***quadrilobate*** *(ELU_1I).* In Jurassic and Cretaceous ammonoids the primary sutures are ***quinquelobate*** *(ELU_2U_1I),* while in the progressive lytoceratids of the Late Cretaceous, the tetragonitids, a ***sexlobate*** primary suture is present (SCHINDEWOLF, 1968).

Within both trends reversions appear, especially in the Cretaceous, and thus a return to *"ceratitic"* or even *"goniatitic"* sutures (e.g., *Neolobites*), as well as reduction of the primary suture of all Cretaceous heteromorphs and *"false hoplitids"* (WIEDMANN, 1966a,b) to the quadrilobate form of the Triassic ammonites (WIEDMANN, 1963, 1965, 1966a). As a basic rule, augmentation of the lobes of Mesozoic ammonites occurs, when not simply by lobal splitting, through the building of umbilical lobes (*"U type"* of SCHINDEWOLF). Adventitious lobes (*A* lobes) are only formed, if ever, at maturity (Arcestidae, Sphenodiscidae).

The consequent advantage of using configuration of the primary suture for large-scale systematic division of the Mesozoic ammonites deserves close attention (Fig. 4). If we treat the Phylloceratina in the manner of SCHINDEWOLF (1968) as the root forms of all Triassic ceratitids, as well as the Jurassic-Cretaceous ammonites, and accept their stratigraphic range as Late Permian to the end of the Cretaceous, then only this suborder includes quadrilobate (e.g., *Leiophyllites*), as well as quinquelobate, forms (all Jurassic-Cretaceous phylloceratids), perhaps even trilobate forms (the Permian Xenodiscidae). Whether in this stem group of Mesozoic ammonites the change of the primary suture coincides with the system boundaries is unknown, since the Triassic phylloceratids, like all Triassic ammonites, have not been investigated sufficiently. Since, however, the unity of these forms is indicated by other characters, such as form of the internal lobe and phylloid saddles, it would be unwise to overrate this continuous transition within the phylloceratids.

The same is true for the sexlobate tetragonitids, which are connected with the lytoceratids not only by a continuous transition (WIEDMANN, 1962a), but also by a major character (e.g., form of the internal *septal lobe*) (WIEDMANN, 1966a,b; 1968). Moreover, since the sexlobate primary suture is apparently first formed within the tetragonitids themselves, it seems more reasonable to regard this group, too, as a superfamily within the Lytoceratina (WIEDMANN, 1962a) rather than as a separate suborder (SCHINDEWOLF, 1967b).

While the Ceratitina are generally admitted to be a natural unit, which SCHINDEWOLF (1968) believed could be linked confidently with the Phylloceratina, the derivation of the Jurassic-Cretaceous Ammonitina from the Lytoceratina or Phylloceratina still presents great difficulty. The previous view supported by LUPPOV & DRUSHCHITS (1958) that the bifid or trifid form of the lateral lobes indicates derivation from the lytoceratids or phylloceratids has become untenable following the proof of both ontogenetic (WIED-

MANN, 1962a, fig. 53) and phylogenetic transition (COBBAN, 1952, fig. 3) from one lobe form to the other, and the discovery of both lobe types on either flank of one suture (WIEDMANN & DIENI, 1968, fig. 45). This is similarly true for the so-called *Suturallobenbildung*[1] (WEDEKIND, 1916), which, according to early opinion of SCHINDEWOLF (1923, 1929, 1961) favored assignment to the phylloceratids *s.l.*, but which in the meantime has been found in both the lytoceratids (WIEDMANN, 1963) and desmoceratids (WIEDMANN, 1966b).

In place of *Suturallobenbildung*, the internal suture, in particular the internal lobe, has assumed importance in this question. SALFELD (1920, 1924) drew attention to presence in the phylloceratids of a simple (unfrilled), double-pointed lituid *I*, but himself doubted the importance of this feature because he believed to have observed an iterative transition between the lituid *I* of the phylloceratids and the normal *I* of the Ammonitina. This was rejected by SCHINDEWOLF (1962) for Jurassic forms and by WIEDMANN (1962b, 1966a,b) for Cretaceous ones, so that today the lituid internal lobe (I_l) can be regarded as the most reliable character of the phylloceratid suture and also of that of the bulk of the Ceratitina. It is thus reasonable to unite both these form groups in the order Phylloceratida as recommended by SCHINDEWOLF. Above all, such a procedure simplifies classification.

SCHINDEWOLF's (1968) recommendation to assign subordinal rank to the pinacoceratids, arcestids, and lobitids is not accepted by us, pending more detailed investigations of the ontogenetic lobe development of Triassic ammonites.

Exceptions, with a denticulated *I*, occur within the thus defined Phylloceratida only in the arcestids, ptychitids, and tragophylloceratids, but all are phylogenetic end forms which contribute nothing to the development of the Ammonitina. The lecanitids, celtitids, and choristoceratids with a single-pointed *I* also do not completely fit into the normal pattern of the Phylloceratida.

In contrast to the above forms in the lytoceratids *s.str.* the septal lobe appears in evolutionary history very early (i.e., in the earliest Liassic). This feature, according to our present knowledge, is exclusively characteristic of the Lytoceratina, in which the I_s can be contrasted with the I_l of the phylloceratids. On the other hand, a denticulated, single- or double-pointed *I* characterizes the Ammonitina and Ancyloceratina, which therefore occupy a kind of intermediate position between phylloceratids and lytoceratids (Fig. 7). If, as suggested by SCHINDEWOLF (1968), the Ammonitina and Ancyloceratina are included with the Lytoceratina in a second order, Lytoceratida (although the phylogenetic connection of these groups is not yet clarified), then the sutural features mentioned above lead to the following diagnoses of the Mesozoic orders and suborders. [Here, and in following parts of the text, primary sutures are marked by an asterisk (*).]

Diagnoses of Mesozoic Orders and Suborders

I. Internal lobe lituid (I_l) .... Order PHYLLOCERATIDA
  1) Primary sutures: $*ELI$ (Permian)→ $*ELU_1I$ (Triassic)→ $*ELU_2U_1I$ (Jurassic-Cretaceous) ..... Suborder PHYLLOCERATINA
  2) Primary suture $*ELU_1I$ .... Suborder CERATITINA

II. Internal lobe not lituid ..... Order LYTOCERATIDA
  1) Primary suture $*ELU_2U_1I$ (Lytoceratoceae) → $*ELU_2U_3U_1I$ (Tetragonitaceae). Septal lobe (I_s) ..... Suborder LYTOCERATINA
  2) Primary suture $*ELU_2U_1I$. Internal lobe simple (I) ..... Suborder AMMONITINA
  3) Primary suture $*ELUI$. Internal lobe simple (I) ..... Suborder ANCYLOCERATINA

Since in Mesozoic ammonoids the external lobe of the adult suture is always bifid, in Jurassic and Cretaceous ammonoids already that of the primary suture, it is simpler to leave out the formula E_1E_1, although this may usefully be applied for Paleozoic forms. The differences in ontogenetic lobe development are of importance for the further division of the Mesozoic ammonoids.

ORDER PHYLLOCERATIDA

The Otoceratoceae, the root stock of the Mesozoic ammonoids, exhibit a lobe development of the formula $*EL(U_1)I \rightarrow ELU_2{:}U_1I_l$ (Fig. 13,*a*) → $ELU_2U_3U_5 : U_1U_1I_l$ (Fig. 13,*c*). Therefore, they are not true phylloceratids in SCHINDEWOLF's (1961) previous interpretation since they lack the so-called *Suturallobenbildung*. SHEVYREV (1968), possibly as a result of similar observations, suggested a new suborder Paraceltitina. The internal lobe of these forms is already lituid, however, so that their inclusion in the Phylloceratina is justified.

From their lobe formula and the little information available on Triassic ammonoids (BRANCO,

[1]This is the more or less symmetrical lobe splitting at the umbilical seam (see Fig. 5).

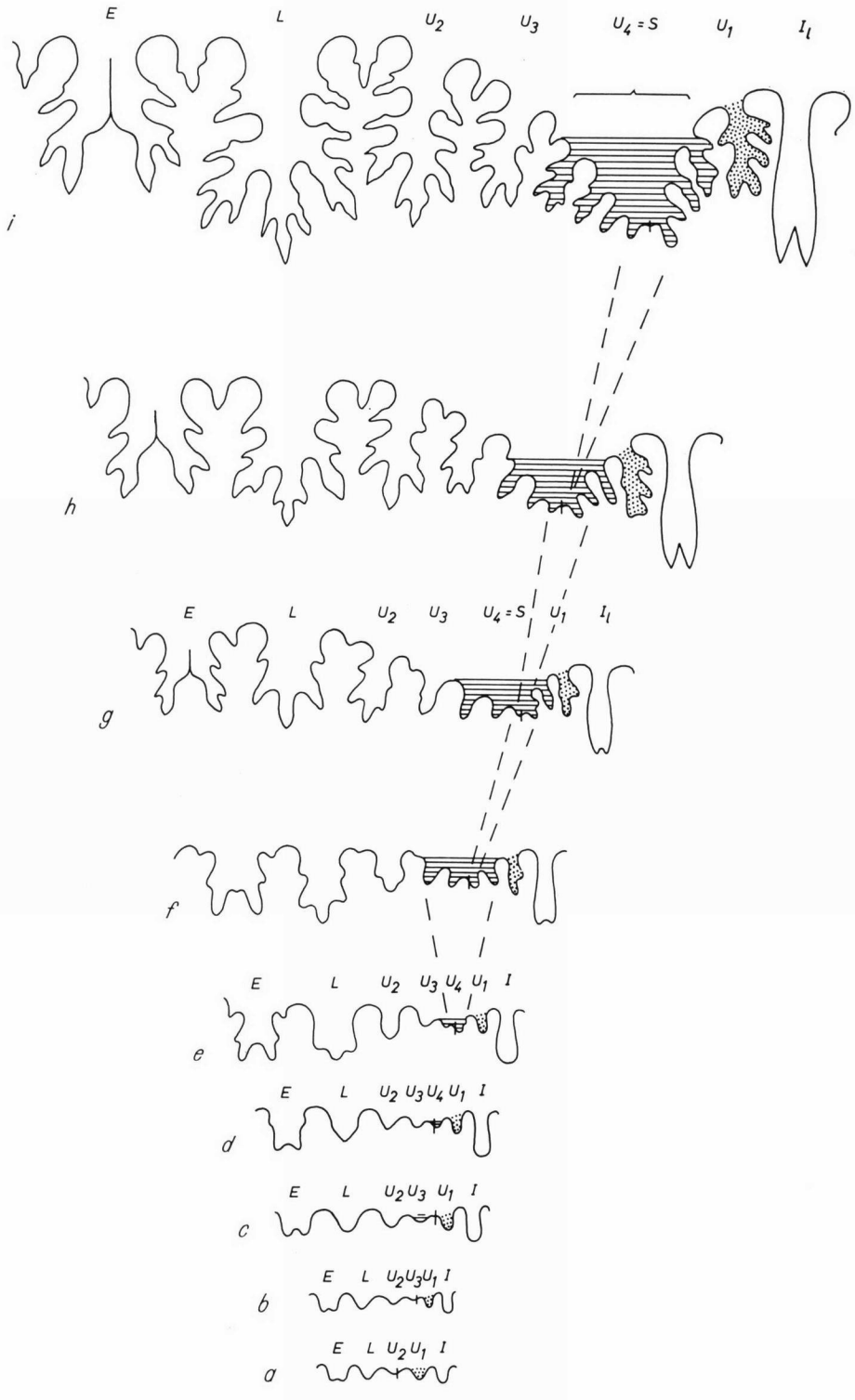

FIG. 5. *(Explanation on facing page.)*

1879; HYATT & SMITH, 1905; SMITH, 1914, 1927, 1932; SCHINDEWOLF, 1929, 1961, 1962, 1968; SHEVYREV, 1961, 1962, 1968; RUZHENTSEV, 1962; ZAKHAROV, 1967; WIEDMANN, 1969b) the following groups can be attached to the Otoceratáceae: Ussuritidae within the phylloceratids (Fig. 13,*e*); Meekoceratáceae including the bulk of the former "Noritaceae"; Clydonitaceae (Fig. 13,*f*); Tropitaceae; Proptychitidae within the "Proptychitaceae" of SHEVYREV; and finally also the Ceratitaceae including the "Hungaritaceae" of SHEVYREV (Fig. 13,*h*, 14,*a*). In the last group an intensive proliferation of the umbilical lobes as far as U_7 or even U_{11} takes place, which makes a separation of these "Ceratitina" from the Phylloceratitina, as suggested by SCHINDEWOLF, possible but not necessary. Also the Triassic heteromorphs (i.e., Choristoceratidae, incl. Cochloceratidae) with the end formula ELU_1I (Fig. 13,*g*) attach themselves easily to this group.

From this type of pure umbilical lobe proliferation a second mode of differentiation of the umbilical suture can be derived easily, and during the course of lobe ontogeny in this only one element is formed at the umbilical seam. However, this element does not, as in the above-discussed forms, originate as a new lobe in the saddle LU_1 (or U_2U_1) but is always inserted on the ventral lobe shoulder of U_1. It is therefore reasonable to label this element U_{1v} (not U_2 or U_3) and to contrast it with the earlier U_{1d}. The resulting lobe formula $EL(U_{1v}{:}U_{1d})I_l$ (Fig. 13,*i*) characterizes the Tirolitidae, Dinaritidae, and Hellenitidae within the "Ceratitaceae," and the Kashmiritidae and Sibiritidae of the "Noritaceae," grouped as the Dinaritaceae by SHEVYREV (1968).

Turning back to the Ussuritidae, some difficulty arises in the interpretation of *Leiophyllites* and the "Palaeophyllitidae" of POPOV. Their lobe formula is somewhat intermediate and may be interpreted as $ELU_2U_3{:}U_1I_l$ as well as $ELU_2U_{1v}{:}U_{1d}I_l$ (Fig. 13,*d*). Probably here, or within the Dinaritaceae, is the point where Lytoceratida with their Triassic forerunners, the Trachyphyllitidae (WIEDMANN, 1966a, 1968), were derived. They portray the lobe formula $ELU_2(U_{1v}{:}U_{1d})I$ (Fig. 14,*f*) and thus in the Triassic, the morphological difference between the lytoceratids and the primitive phylloceratids is very small: only the denticulate I (without septal lobe) and the greater degree of suture frilling (especially of the saddles) of *Trachyphyllites* are different from the suture of palaeophyllitids.

Suturallobenbildung in U_3 or U_4 (Fig. 5), regarded by SCHINDEWOLF as typical of the phylloceratids, first occurs in younger phylloceratids, the Discophyllitidae (incl. Juraphyllitidae) and Phylloceratidae, and these families continue unchanged to the end of the Cretaceous. The lobe formulas $ELU_2(U_3 = S)U_1I_l$ and $ELU_2U_3(U_4{=}S)U_1I_l$ (Fig. 15,*a*) are varied only slightly in *Tragophylloceras* through the weak frilling of I as mentioned above. On the whole, the phylloceratids represent an exceptionally conservative group extending from the Carnian to the Maastrichtian (except for progressive frilling of the phylloid saddles). Where exactly the transition from a quadrilobate to a quinquelobate primary suture took place is not known, although it must be in the neighborhood of the Triassic-Jurassic boundary.

It is noteworthy from their lobe formula $ELU_2(U_3{=}S,\ 10{:}10)U_1I_l$ (Fig. 14,*c*) that the Megaphyllitidae lie very close to the phylloceratids. The *Suturallobenbildung* within U_3 shows an extreme frilling with more than 20 incisions symmetrically distributed on either side of the umbilical seam. This does not apply to *Procarnites* which shows asymmetrical *Suturallobenbildung* within U_3 (e.g., *Ptychophylloceras* in SCHINDEWOLF, 1961, fig. 29, 30). This asymmetry can be expressed in the formula $ELU_2(U_3{=}S,\ 7{:}4)U_1I_l$ (Fig. 13,*k*). *Procarnites*, selected as type of a new family by CHAO (1959), was placed in the Proptychitaceae by SHEVYREV (1968).

The Ptychitaceae with their lobe formula $ELU_2(U_3{=}S,\ 8{:}8)U_1I$ (Fig. 14,*e*) can also be placed close to the forms mentioned above, especially the Megaphyllitidae with their similarly symmetrical *Suturallobenbildung*, differing distinctly in the stronger frilling of the saddles and internal lobe. These characters associate the ptychitids with the Arcestidae, in which, however, no *Suturallobus* appears to be present. Instead, a quinquelobate primary suture (SCHINDEWOLF, 1929) and the formation of adventitious (A) and internal umbilical lobes (U_n) in the saddle U_1I, otherwise unknown in Triassic forms, occurs

FIG. 5. Suture ontogeny and *Suturallobenbildung* in U_4 of phylloceratids: *Sowerbyceras (Holcophylloceras) calypso* (D'ORBIGNY), Lower Cretaceous (Valanginian), France (from Wiedmann, 1968). [*a*, primary suture; *i*, adult suture at whorl height of 3 mm.]

(Schindewolf, 1968). The arcestids, with their resulting lobe development

$$*ELU_2U_1I \rightarrow EALU_2U_3U_1U_{nv}U_{nd}I$$

(Fig. 14,*d*), stand markedly apart from the otherwise very uniform character of the Triassic ammonoids.

Similarly, the Lobitidae, with lobe-splitting in the elements *L*, U_2 and U_1 according to the formula $E\,(L_vL_d)\,(U_{2v}U_{2d})\,U_3 : U_{1v}U_{1d}I_1$ (Fig. 14,*b*) also occupy a special position.

The lobe development of the phylogenetically unimportant pinacoceratids unfortunately has not been sufficiently investigated.

Thus the most essential types of lobe formation found among Jurassic-Cretaceous ammonites and about which much new information has recently been published (especially by Mikhailova, 1957, 1958, 1960, 1963; Beznosov, 1960; Schindewolf, 1961-68; Wiedmann, 1962a, 1963, 1965, 1966a,b, 1968, 1969a) were already present in Triassic forms.

ORDER LYTOCERATIDA

As already mentioned, the formation of the septal lobe in *I* (I_s) is a qualitatively new feature in the lytoceratids which is found occurring as early as the early Liassic. The lobe formula of the Lytoceratidae, $ELU_2\,(U_{1v} : U_{1d})\,I_s$ (Fig. 6, 14,*g*), can be derived easily from the Triassic Trachyphyllitidae. The same is true for the sexlobate primary suture of the Tetragonitaceae, direct derivatives of the Lytoceratidae. In this case the formation of a massive suspensive lobe in U_1 occurs first in the Gaudryceratidae (Fig.

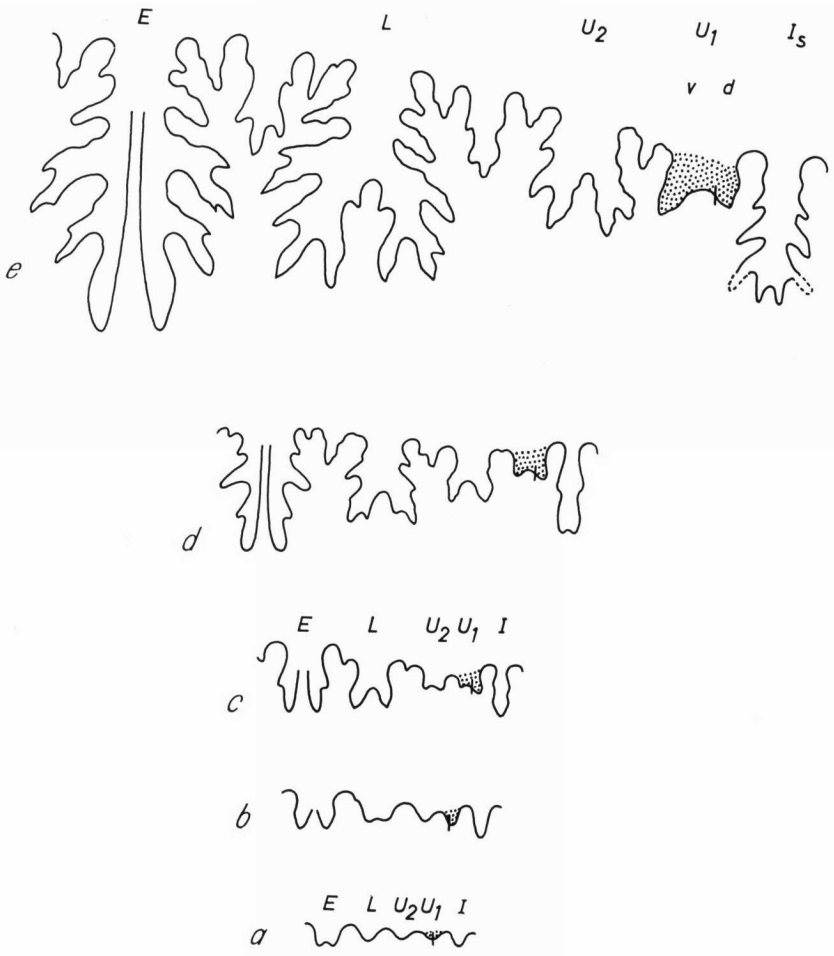

Fig. 6. Suture ontogeny of true lytoceratids with I_s and subdivided U_1: *Lytoceras juilleti* (d'Orbigny), Lower Cretaceous (Valanginian), France (after Wiedmann, 1968). [*a*, primary suture; *e*, adult suture a whorl height of 2 mm.; stippled, septal lobe.]

14,*h*), and proceeds to a *Suturallobenbildung* in U_4 in the Tetragonitidae (Fig. 14,*i*), indicating convergence with the phylloceratids (WIEDMANN, 1963): $ELU_2U_1I_8 \rightarrow ELU_2U_3(U_4{=}S,\ 2{:}2)U_1I_8$.

According to SCHINDEWOLF's (1962) most recent investigations, the psiloceratids, which represent the root stock of the Jurassic and Cretaceous Ammonitina with quinquelobate primary suture, have no *Suturallobenbildung*. Instead, a very early division of U_1 occurs. The resulting lobe formulas $ELU_2U_3{:}U_{1v}U_{1d}I \rightarrow ELU_2U_3U_4U_5{:}U_{1v}U_{1d}I$ were derived by SCHINDEWOLF (1962) from an unknown lytoceratid root. More important than the as yet not fully clarified question of the root of the psiloceratids—at or near the point of divergence of the lytoceratids from the phylloceratid main stock—is the fact that all younger Ammonitina can be easily linked to the psiloceratids. SCHINDEWOLF's studies of lobe ontogeny thus indicate that the Ammonitina form a monophyletic unit.

The lobe formula of the Eoderoceratacеae, $ELU_2U_3{:}U_{1v}U_{1d}$ (Fig. 15,*c*), is so closely similar to that of the Psiloceratacеae that SCHINDEWOLF even considered uniting these two superfamilies, thought by SPATH (1938) and ARKELL (1950, 1957) to be diphyletic. Perfect identity of sutures is found among the Psiloceratidae, Polymorphitidae, Amaltheidae, and Dactylioceratidae.

In addition, fusion of the ventral and dorsal part of U_1 may occur in both superfamilies (in SCHINDEWOLF's opinion always secondary fusion, i.e., in the Arietitidae, Echioceratidae, Oxynoticeratidae, Phricodoceratidae, and Aegoceratidae [including *Androgynoceras* and *Oistoceras*]), all of which have the common lobe development $*ELU_2U_1I \rightarrow ELU_2U_3{:}U_1I \rightarrow ELU_2{:}U_1I$ (Fig. 15,*d*). Additionally, as a slight modification of SCHINDEWOLF's views, *Suturallobenbildung* may occur in U_{1v} according to the formula $ELU_2(U_{1v}{=}S)U_{1d}I$ in the psiloceratids and eoderoceratids (i.e., in the Cymbitidae and the Liparoceratidae, for which SPATH, 1923, probably erroneously, assumed a phylogenetic relationship). Basing his opinion on the yet unproven assumption that a secondarily fused U_1 may not split again, SCHINDEWOLF (1964) believed the Hildoceratacеae to be diphyletic. He restricted the superfamily to include only the Arieticeratidae, Hildoceratidae, and Harpoceratidae having the lobe development $ELU_2U_3{:}U_1I \rightarrow ELU_2U_3U_5{:}U_4U_1I \rightarrow ELU_2U_3U_5U_7U_9U_{11}U_{12}{:}U_{10}U_8U_6U_4U_1I$ (Fig. 15,*e*) and placed them as the descendants of the Aegoceratidae. The Hammatoceratidae, Paroniceratidae, and Dumortieriidae with the lobe formulas $ELU_2U_3U_4{:}(U_{1v}U_{1d})I$ (Fig. 15,*f*) $\rightarrow ELU_2U_3U_4{:}U_1I$ were regarded as the root of the Hammatoceratacеae, derived from Dactylioceratidae still having a split U_1. These opinions of SCHINDEWOLF resulted, moreover, in the subdivision of the previously homogeneous Haploceratacеae: the oppeliids with an undivided U_1 being placed in the Hammatoceratacеae while forms with (according to SCHINDEWOLF) a "secondarily undivided" U_1 were grouped as Haploceratacеae. These comprise the bulk of the graphoceratids, strigoceratids, and sonniniids, as well as the true haploceratids and a large part of the Cretaceous oppeliids. Perhaps a simpler classification would be based on the assumption that a repeated oscillation between an undivided and divided U_1 occurred (Fig. 7). Certainly, oppeliid and haploceratid sutures are closely similar in their strong proliferation of lobes, but the differing fate of U_1 seems to be a radical point of difference which can be seen in the lobe formulas which for Oppeliidae are $ELU_2U_3U_4U_5U_7{:}U_8U_6U_{1v}U_{1d}I \rightarrow ELU_2U_3U_4U_5U_7U_9U_{11}U_{13}{:}U_{12}U_{10}U_8U_6U_{1v}U_{1d}I$ (Fig. 15,*g*), and for Haploceratidae $ELU_2U_3U_5U_7U_8{:}U_6U_4U_1I$ (Fig. 15,*k*).

While the suture of the Phlycticeratidae $(ELU_2U_3{:}U_{1v}U_{1d}I)$ can be compared closely with that of the oppeliids, those of the Strigoceratidae, Mazapilitinae, and Aconeceratinae are identical with that of the haploceratids: $ELU_2U_3U_5{:}U_4U_1I$ (Strigoceratidae), $ELU_2U_3U_5U_7U_9{:}U_8U_6U_4U_1I$ (Aconeceratinae).

Whereas the oppeliids also were traced directly back to the hammatoceratids by SCHINDEWOLF, the haploceratids were derived from the dumortieriids already discussed, via the Graphoceratidae and Sonniniidae with the lobe formulas

$$ELU_2U_3U_5{:}U_6U_4U_1I$$
$$ELU_2U_3U_5U_7U_9U_{11}U_{10}U_8U_6U_4U_1I$$

(see Fig. 15,*i*). The boundary between the two superfamilies divides the graphoceratids with "primary divided" U_1 (Dumortieriidae) from the graphoceratids and sonniniids with "secondary undivided" U_1. In contrast the Tmetoceratidae with a probable lobe formula $ELU_2U_1{:}I$ (see Fig. 15,*h*) were regarded as end members (with undivided U_1) of the Hammatoceratacеae, comparable to the Arietitidae, Echioceratidae, or Aegoceratidae of the Psiloceratacеae.

The Otoitidae, earliest representatives of the

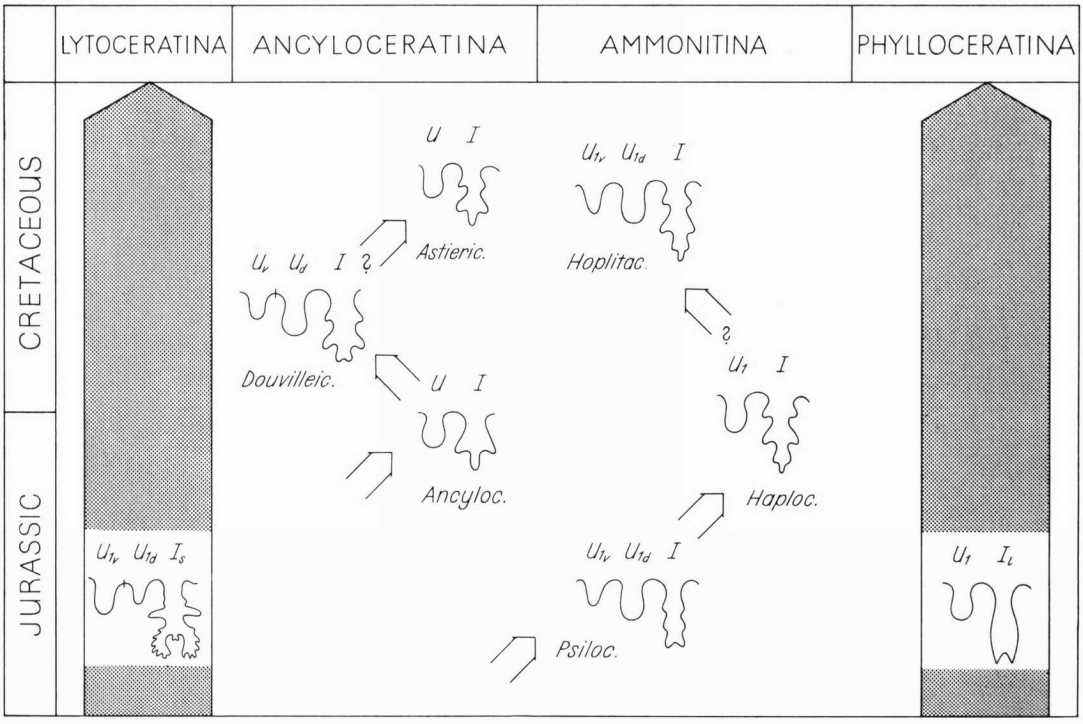

FIG. 7. Phylogeny of elements *I* and U_1 within Jurassic-Cretaceous ammonites (after Wiedmann, 1966b). [*Psiloc.*= Psiloceratáceae, *Haploc.*=Haploceratáceae, *Hoplitac.*=Hoplitaceae, *Ancyloc.*=Ancyloceratáceae, *Douvilleic.*=Douvilleiceratidae, *Astieric.*=Astiericeratidae.]

stephanoceratids, also show a division of U_1, indicating their origin in the Hammatoceratáceae. This division is already reversed in the almost simultaneously appearing Stephanoceratidae and Sphaeroceratidae, just as in the bulk of the Stephanoceratáceae. Nevertheless, all these forms are united by the possession of a U_n unique to the stephanoceratids. Consideration of only the adult suture is insufficient for the understanding of these sutures (Fig. 8).

In labelling the lobe peculiarly situated in the saddle U_1I, as "U_n" SCHINDEWOLF (1965) retreated from his earlier (1923) interpretation of this element as a "heterochronous U_1." Study of the numerous lobe pictures published by SCHINDEWOLF raises the suspicion that this element, almost always (except in the Otoitidae) found on the lobe shoulder of an undivided U_1, does not correspond to a heterochronous U_1, but may perhaps be a heterochronous U_{1d}. This would explain why a U_n is never found in the closely related Perisphinctaceae, with an almost universally present divided U_1. Thus derivation of Perisphinctaceae from Stephanoceratáceae seems more likely than that from Hammatoceratáceae (SCHINDEWOLF, 1966).

In contrast to the very homogenous Perisphinctaceae, the Stephanoceratáceae show a notably large variation in configuration of the suture. The original otoitid suture ELU_2U_3:$(U_{1v}U_{1d})U_nI$ (Fig. 16,*a*) → $ELU_2U_3U_4$:$U_5(U_{1v}$:$U_{1d})U_nI$ → $ELU_2U_3U_5$:$U_4U_1U_nI$ is replaced in the majority of the stephanoceratids (i.e., Stephanoceratidae, Sphaeroceratidae, Macrocephalitidae, Pachyceratidae, Oecoptychiidae, Kosmoceratidae, Cardioceratidae, Morphoceratidae) by the lobe formulas $ELU_2U_3U_5$:$U_4U_1U_nI$ (Fig. 16,*b*)→ELU_2:U_3U_1I (Fig. 16,*d*). In the pachyceratids and the oecoptychiids the division of U_1, as well as the U_n, are reduced. Also, for the Parkinsoniidae a lobe formula $ELU_2U_3U_5$:$U_4U_1U_nI$ (Fig. 16,*e*) was assigned and thus supported their attachment to the Stephanoceratáceae (SCHINDEWOLF, 1965), although in this case the identity of U_n and U_{1d} (e.g., *op.cit.*, fig. 288) and thus the possibility of a perisphinctid formula $ELU_2U_3U_5$:$U_4U_{1v}U_{1d}I$ cannot always be denied confidently. The Spiroceratidae (incl. Acuariceratidae) with their curious

ontogenetic lobe reduction restricted to this heteromorph group $*ELU_2U_1I \rightarrow ELU_2I$ or EU_2I (Fig. 16,*f*) were correctly placed as descendants of the parkinsoniids. A special development within the Stephanocerataceae are the Tulitidae without U_n, undivided U_1, and with weak *Suturallobenbildung* in U_3. They demonstrate once again the restricted phylogenetic importance of this feature: $ELU_2(U_3{=}S)U_1I$ (Fig. 16,*c*). Following their suture formulas, the Tulitidae, Pachyceratidae

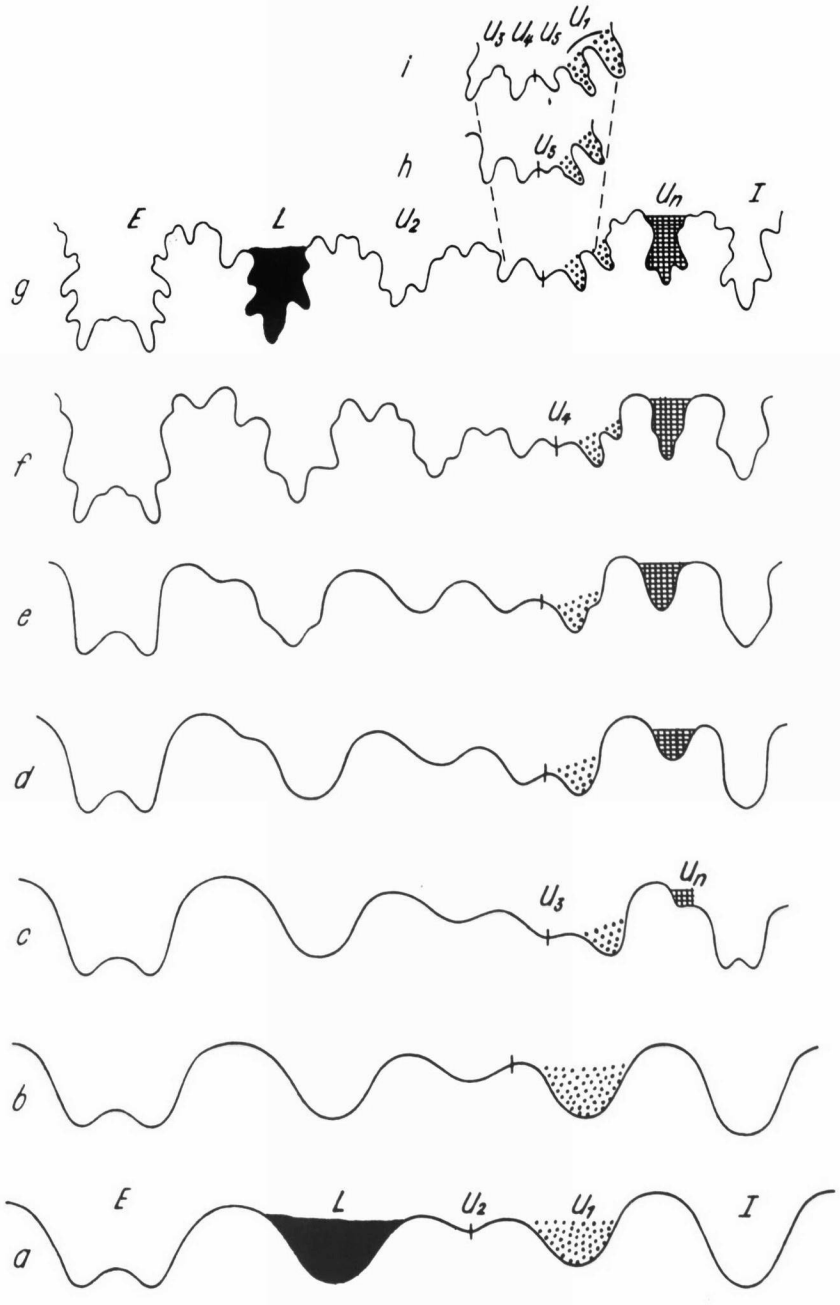

FIG. 8. Suture ontogeny of stephanoceratids with U_n and subdivided U_1: *Otoites* sp. cf. *O. tumulosus* WESTERMANN, Middle Jurassic (middle Bajocian), England (from Schindewolf, 1965). [*a*, primary suture; *g*, adult suture at whorl height of 2.5 mm.; *i*, at height of 5.8 mm.]

and "Oecoptychiidae" may be placed likewise within the Perisphinctaceae. New investigations about this point are needed. For the majority of the Perisphinctaceae the lobe formula $ELU_2U_3(U_4{=}S)U_{1v}U_{1d}I$ is applicable (Fig. 16,*g*), but in the Simoceratidae $(ELU_2U_3{:}U_{1v}U_{1d}I)$ the *Suturallobenbildung* is reduced, and in the Endemoceratidae, Aspidoceratidae, Peltoceratidae, and Oosterellidae also the splitting of U_1: $ELU_2U_3U_1U_1I$ (Fig. 16,*h*). In their suture formula $ELU_2(U_3{=}S)U_1I$ the Holcodiscidae show greater affinity with the Perisphinctaceae than with the Desmoceratacеae (Wiedmann, 1966b).

Within these desmoceratacеans, forms with and without division of U_1 appear simultaneously. Those with an undivided U_1 and with the lobe formula $ELU_2U_3U_5U_7{:}U_6U_4U_1I$ (Fig. 16,*i*) are here the older (Eodesmoceratinae), which led to the suggestion of the derivation of the Desmoceratacеae from the haploceratids (Wiedmann, 1966a). The Pulchelliidae with their suture development $*ELU_2U_1I{\rightarrow}ELU_2U_3U_5U_7{:}U_8U_6U_4U_1I$ appear to follow directly, and similarly, all of the Acanthoceratacеae for which the analogous formula $ELU_2U_3U_5{:}U_6U_4U_1I$ (Fig. 16,*l*) is characteristic. The formation of adventitious lobes *(A)* within the Sphenodiscidae is a slight deviation from this scheme.

All younger desmoceratids (Desmoceratinae, Puzosiinae), as well as the Silesitidae, Kossmaticeratidae, Pachydiscidae, and above all most of the Hoplitaceae, differ from the above in the *Suturallobenbildung* in U_4 and a splitting of U_1. The extraordinarily constant lobe formula common to all these forms is $ELU_2U_3(U_4{=}S)U_{1v}U_{1d}I$ (Fig. 16,*k*), which demonstrates the necessity to unite the "Desmoceratacеae" and Hoplitaceae (Wiedmann, 1966b). While Wiedmann, on the basis of continuous transition between eodesmoceratids and desmoceratids, supported the view that all Hoplitaceae were rooted in the haploceratids and that therefore a new transition from an undivided to a divided U_1 occurred (Fig. 7), Schindewolf (1966) again held such a regeneration or reversion to be impossible. He derived all younger desmoceratids and hoplitids from perisphinctid forms with a "still original" U_1. The Acanthoceratacеae, however, represent, in Schindewolf's opinion, phylogenetic end forms of the desmoceratids or direct descendants of the haploceratids (Schindewolf, 1967a).

More significant than these discrepancies, for the solution of which further investigations are required is the fact that the Cretaceous Ammonitina as a whole can now be traced back to their Jurassic forerunners and not linked to the phylloceratids or lytoceratids, as accepted by Wright (1955, 1957) and Casey (1957, 1961). Also important for this conclusion was the observation that no transition exists between the lituid *I* of the phylloceratids and the denticulate *I* of the Cretaceous Ammonitina (Wiedmann, 1962b, 1966a).

A subject of special interest which illustrates the overriding importance of lobe ontogeny is that of the so-called Cretaceous heteromorphs and their derivatives. Contrary to their present widespread interpretation as a polyphyletic collection of phylogenetic end forms, recently all these heteromorphs have been shown to be characterized by a quadrilobate primary suture (Wiedmann, 1963, 1965, 1966b, 1969a). This makes a monophyletic origin probable, at least for the Ancyloceratacеae (incl. Turrilitacеae): $*ELUI{\rightarrow}ELUI$ (Fig. 9,*1*). Since the change from a quinquelobate to a quadrilobate primary suture took place suddenly, transitional forms are hardly to be expected. From their general evolute shell habit and scarcity of suture elements the root forms are most likely to be present among the lytoceratids, although origin in the Jurassic Ammonitina, as derivatives of Lytoceratina, can no longer be ruled out today.

The Scaphitaceae also exhibit a quadrilobate primary suture (Wiedmann, 1965). From phylogeny as well as lobe ontogeny of this group it has become clear (*op.cit.*, fig. 14, 15) that the regenerated lobes in the saddle *LU* observed by Schindewolf (1961, 1968) are in reality homologous with the saddle frills of the root form *Eoscaphites*. Therefore they were called *pseudolobes* by Wiedmann (1965) and labelled *p*. Thus the lobe development of the Scaphitaceae fits without difficulty into the general pattern of the Cretaceous heteromorphs: $*ELUI{\rightarrow}ELp_1p_2p_3{:}U_vU_dI$ (Fig. 9,*2*). This view is supported by the open initial whorl of *Eoscaphites*.

More surprising was the observation that a quadrilobate primary suture is also present in some Hoplitaceae, the so-called "false hoplitids" (i.e., Douvilleiceratidae, Cheloniceratidae, Parahoplitidae, Acanthohoplitidae, Astiericeratidae, Trochleiceratidae, Mathoceratidae, Deshayesitidae). Thus in the Trochleiceratidae, which were classified with the Pulchellidae by Wright (1957), a lobe development according to the "heteromorph

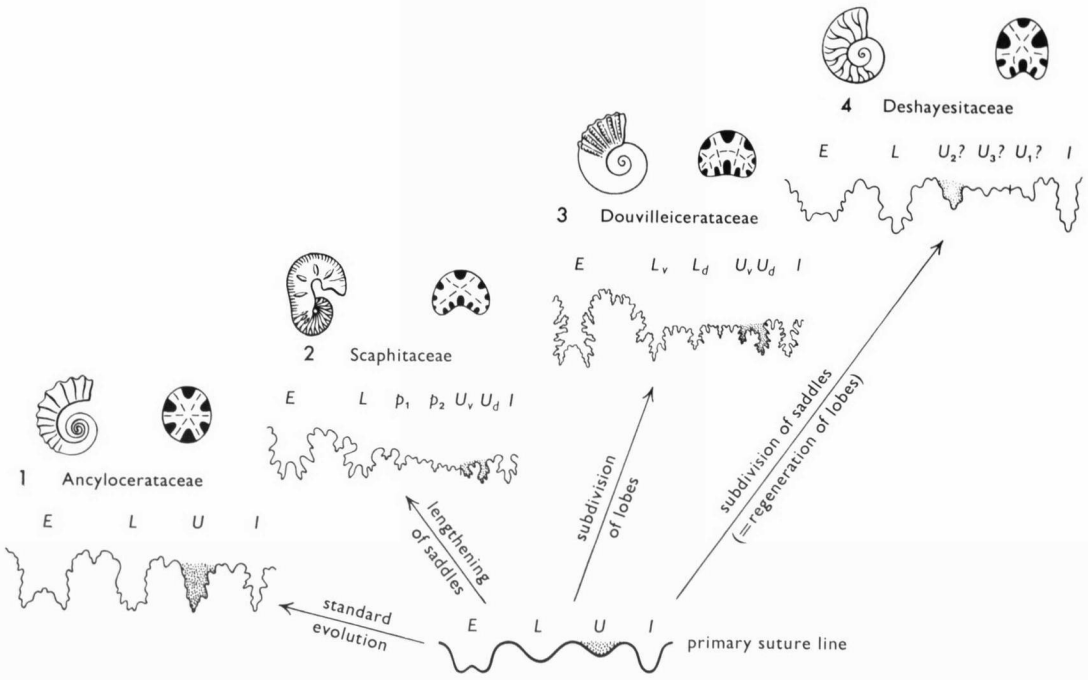

FIG. 9. Different types of suture ontogeny in Ancyloceratina.——*1*. Standard evolution of Cretaceous heteromorphs (Ancyloceratacеae).——*2*. Suture development by lengthening of saddle *LU*, insertion of "pseudolobes" *(p)* and subdivision of U_1 (Scaphitaceae).——*3*. Suture development by subdivision of the lobes *L* and *U* (Douvilleiceratacеae). ——*4*. Suture development by subdivision of saddle $U_2?I$=lobe regeneration (Deshayesitaceae).

formula" $*ELUI \rightarrow ELUI$ was found (WIEDMANN, 1963); in the Douvilleiceratidae the suture development is expressed by the formulas $*ELUI \rightarrow EL_vL_dU_v{:}U_dI$ (Fig. 9,*3*), and in the Parahoplitidae by the analogous formulas $*ELUI \rightarrow ELU_v{:}U_dI$ (Fig. 10) or $ELU_{vv}U_{vd}{:}U_dI$ (WIEDMANN, 1966b). Final proof that these Douvilleiceratacеae also are derivatives of the heteromorphs, probably the leptoceratids, was demonstration of an open first whorl in the oldest douvilleiceratid genus *Paraspiticeras* by WIEDMANN (1966b, pl. 4, fig. 2a).

The Deshayesitidae, which belong to the same form group of "false hoplitids," even show a genuine lobe regeneration according to the formulas $*ELU_2?I \rightarrow ELU_2?U_3?{:}\ U_1?I$ (Fig. 9,*4*). Thus a separate origin in late Barremian heteromorphs *(Hemihoplites)* can be assumed for this form group proposed as distinct superfamily Deshayesitaceae (WIEDMANN, 1966b). Independently, TOVBINA (1965) considered the heteroceratid genus *Colchidites* to be a possible ancestor. This apparent discrepancy could be resolved, if WIEDMANN's (1966b, p. 45) assumption of identity of these two genera could be proved. Since all these "false hoplitids" show an extraordinary convergence to the genuine hoplitids in their involution, sculpture, and even in apparent complexity of the adult suture, their evolutionary role probably would not have been recognized without consideration of lobe ontogeny. Figure 9 gives an impression of the identity, as well as diversity, of the well-defined heteromorph suture within the four superfamilies now included here.

At this point the inadequacy of the Soviet lobe terminology becomes evident. Because of its complexity and inability to bring out homologies, relationships of the Douvilleiceratacеae remained obscure even though thorough investigations of lobe patterns had been made by MIKHAILOVA (1957, 1958, 1960, 1963). A short comparison of lobe formulas selected from recent Soviet (MIKHAILOVA, 1960; RUZHENTSEV, 1960, 1962; SHEVYREV, 1960) and German papers (SCHINDEWOLF, 1961-68; WIEDMANN, 1963, 1965, 1966a,b) should make this clear (Table 2).

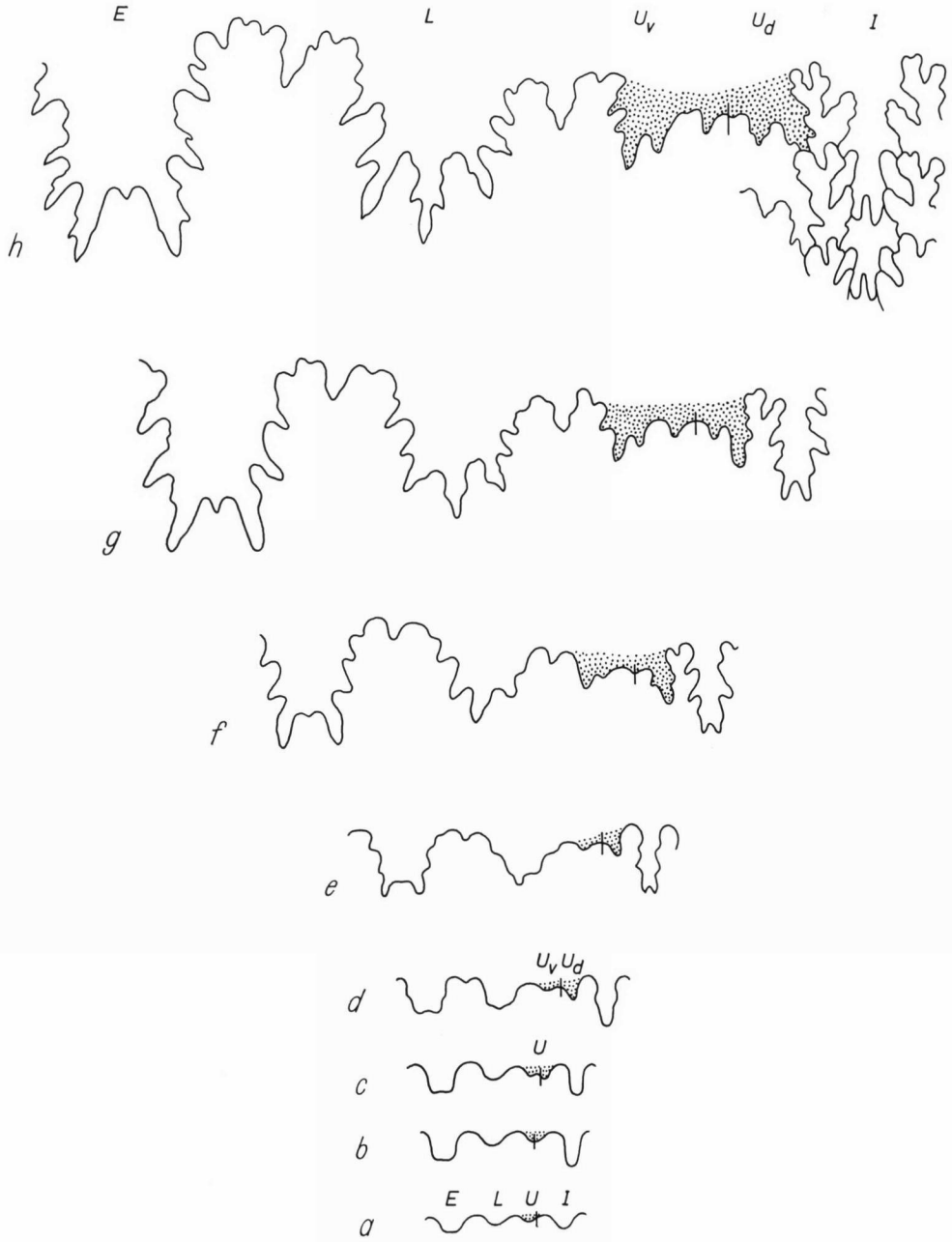

FIG. 10. Suture ontogeny of a "false hoplitid": *Gargasiceras gargasense* (D'ORBIGNY), Lower Cretaceous (Aptian), France (from Wiedmann, 1966b). [*a*, primary suture; *h*, adult suture at whorl height of 4.5 mm.]

TABLE 2. *Comparison of Suture Formulas*

	WEDEKIND's terminology	RUZHENTSEV's terminology
Phylloceras	$ELU_2U_3(U_4{=}S)U_1I_1$	$(V_1V_1)UU^1U^3U^4U^6U^7U^9U^{11}U^{12}U^{13}{:}U^{10}U^8U^5U^3ID$
Lytoceras	$ELU_2(U_{1v}{:}U_{1d})I_2$	$(V_1V_1)UU^1I_1{:}I_1D$
Schlotheimia	$ELU_2U_3U_4U_5{:}U_{1v}U_{1d}I$	$(V_1V_1)UU^1U^2U^3U^4{:}I_2I_1D$
Hammatoceras	$ELU_2U_3U_4{:}(U_{1v}U_{1d})I$	$(V_1V_1)UU^1U^2U^3{:}U^4I_1I_2D$
Oppelia	$ELU_2U_3U_4U_5U_7{:}U_6U_{1v}U_{1d}I$	$(V_1V_1)UU^1U^2U^3U^4U^6{:}U^5I_1I_2D$
Cadoceras	$ELU_2U_3U_4{:}U_5U_1U_nI$	$(V_1V_1)UU^1U^2U_1{}^3U^4{:}U_1{}^3II^1D$
Macrocephalites	$ELU_2U_3U_4{:}U_5U_1U_nI$	$(V_1V_1)UU^1U^2U^3{:}U^4II^1D$
Polyplectites	$ELU_2U_3{:}U_1U_nI$	$(V_1V_1)UU^1I_2{:}I_1I^1D$
Kosmoceras	$ELU_2U_3U_4U_1U_nI$	$(V_1V_1)UU^1I_1I^2I^3{:}I^4I_1I^1D$
Strenoceras	$ELU_2U_3U_4U_{1v}U_{1d}I$	$(V_1V_1)UU^1U^2{:}U^3ID$
Perisphinctes	$ELU_2U_3(U_4{=}S)U_{1v}U_{1d}I$	$(V_1V_1)UU^1U_1{}^2{:}U_1{}^2ID$
"Pseudoperisphinctes"	$ELU_2U_3(U_4{=}S)U_{1v}U_{1d}I$	$(V_1V_1)UU^1U^2U_1{}^3....U_1{}^3I_1I_2D$
Grossouvria	$ELU_2U_3(U_4{=}S)U_{1v}U_{1d}I$	$(V_1V_1)UU^1U_1{}^2U_1{}^3U_1{}^4{:}U_1{}^4U_1{}^3U_1{}^2ID$
Craspedites	$ELU_2U_3(U_4{=}S)U_{1v}U_{1d}I$	$(V_1V_1)UU^1U_1{}^2U_1{}^3U_1{}^4U_1{}^5{:}U_1{}^5U_1{}^4U_1{}^3U_1{}^2ID$
Cheloniceras	$EL_vL_dU_v{:}U_dI$	$(V_1V_1)UU_2U^1I_2{:}I_1D$
Colombiceras	$ELU_v{:}U_dI$	$(V_1V_1)UU^1{:}ID$
Acanthohoplites	$ELU_{vv}U_{vd}{:}U_dI$	$(V_1V_1)UU^1U^2U^3{:}ID$
Hypacanthoplites	$ELU_{vv}U_{vd}{:}U_dI$	$(V_1V_1)UU^1U_1{}^2{:}U_1{}^2ID$
Deshayesites	$ELU_2?U_3?{:}U_1?I$	$(V_1V_1)UII^2{:}I^3I^1D$

As indicated by Table 2 the Soviet terminology for the closely related genera *"Pseudoperisphinctes"* and *Grossouvria* shows neither mutual agreement nor formulas comparable with *Perisphinctes*. *"Pseudoperisphinctes,"* however, can be compared with *Cadoceras,* and *Grossouvria* with *Craspedites*. *Craspedites* itself shows more agreement with *Schlotheimia* than with any of the closely related genera *Macrocephalites, Strenoceras,* or *Kosmoceras*. Within the Stephanocerataceae the Soviet terminology shows extraordinary convergence, while on the other hand much greater agreement appears to exist with certain "false hoplitids" (*Macrocephalites-Colombiceras, Polyplectites-Cheloniceras,* or *Deshayesites*). The lytoceratid suture shows most affinity with the polyplectid suture, and that of the phylloceratids with the oppeliids. For example, particular attention should be directed to the difference in Soviet terminology between the sutures of the "false hoplitids" *Acanthohoplites* and *Hypacanthoplites* which in reality are identical. Instead, the lobe formula of *Hypacanthoplites* shows perfect agreement with that of *Perisphinctes*.

This short review should show that only a completely morphogenetically based lobe terminology, such as that proposed by WEDEKIND, can differentiate homologous and convergent elements. Only from a scheme of this kind can new phylogenetic knowledge be expected. We must, of course, realize that any terminology is no more than an aid to facilitate communication concerning an often extremely complicated set of facts. The system which is simplest and above all most accurate will always be preferable. The ambition to produce new and more complicated terminologies should not be allowed to disturb what after all must be the goal of every terminology: international understanding. It would be very regrettable if the continuing controversy over lobe terminologies should damage the reputation of lobe-ontogeny studies without bringing nearer realization of mutual wishes for a natural system of ammonoid classification.

SURVEY OF SUTURAL DEVELOPMENT IN SUPERFAMILIES

The presently understood sutural development in ammonoid superfamilies is outlined in the following tabulation. Sutural formula of primary suture is marked by an asterisk (*).

I. Order Goniatitida
Suborder Anarcestina — Families
1. Anarcestaceae
a. *EL, ELI,→ELUI,→EALU$_2$U$_1$I* (Fig. 11,*a*) ..... Mimoceratidae, Anarcestidae, a.o.
b. *ELI,→(E$_1$E$_2$E$_m$E$_2$E$_1$)LI* (Fig. 11,*b*) ..... Auguritidae

2. Pharciceratacea
   a. $*ELI \rightarrow (E_1E_mE_1)LI, \rightarrow (E_1E_mE_1)LUI$ (Fig. 11,*c*)
      $\rightarrow (E_1E_mE_1)LU_2U_3 \ldots U_1I$ ..... Gephuroceratidae
      Pharciceratidae
   b. $*ELI \rightarrow E_xE_mE_xLU_yI$ [E_x=up to E_7, U_y=up to U_{18}] (Fig. 11,*d*) ..... Beloceratidae
3. $ELI, \rightarrow ELU(I_1I_1)$ (Fig. 11,*e*) ..... Prolobitaceae

Suborder Goniatitina

4. $*ELI \rightarrow EALI, \rightarrow EALUI, \rightarrow EA_3A_2A_1LUI$ (Fig. 11,*f*) ..... Cheiloceratacea
5. Goniatitaceae
   a. $*ELI \rightarrow (E_1E_mE_1)ALUI$ (Fig. 11,*g*) ..... Goniatitidae, Gastrioceratidae, Paragastrioceratidae
   b. Same as a, $L \rightarrow (L_vL_mL_d), \rightarrow L_vL_mL_d$ (Fig. 11,*h*) ..... Metalegoceratidae
   c. Same as a, $U_2 \rightarrow (U_{2v}U_{2m}U_{2d}), \rightarrow U_{2v}U_{2m}U_{2d}$ (Fig. 11,*i*) ..... Schistoceratidae
6. Agathiceratacea
   a. $*ELI \rightarrow (E_1E_mE_1)ALUI \rightarrow$trifurcation of E_1 and A (Fig. 11,*k*) ..... Delepinoceratidae
   b. Same as a, trifurcation of A:$\rightarrow$
      $(E_1E_mE_1)A_vA_mA_dL{:}UI$ (Fig. 12,*a*) ..... Agathiceratidae
7. Shumarditaceae
   a. $*ELI \rightarrow (E_1E_mE_1)ALUI \rightarrow$simple trifurcation in A, L and I, repeated trifurcation in A and U (Fig. 2) ..... Shumarditidae, Marathonitidae
   b. Same as a, repeated trifurcation of A, L, and U ..... Cyclolobidae
   c. Same as a, trifurcation of A and U, furthermore insertion of other A and U (Fig. 12,*b*) ..... Popanoceratidae
8. Dimorphoceratacea
   a. $*ELI \rightarrow (E_1E_mE_1)ALUI \rightarrow$denticulation of individual lobes ..... Thalassoceratidae
   b. Same as a, however more or less irregular bifurcation of E and A (Fig. 12,*c*) ..... Dimorphoceratidae
   c. Same as a, $\rightarrow (E_1E_2E_mE_2E_1)AL{:}UI$ (Fig. 12,*d*) ..... Neodimorphoceratidae
9. $*ELI \rightarrow (E_1E_mE_1)ALUI \rightarrow (E_1E_mE_1)AL(U_2{=}S)U_1I$, $\rightarrow$further insertion of U, the last $U{=}S$ (Fig. 12,*e*) ..... Adrianitaceae

Suborder Prolecanitina

10. Prolecanitaceae
    a. $*ELI \rightarrow ELU_2U_1I, \rightarrow$increase of U up to 7 (Fig. 12,*f*) ..... Prolecanitidae
    b. Same as a, $\rightarrow (E_1E_mE_1)LU_2U_1I$, increase of U up to U_9, denticulation of individual lobes ..... Daraelitidae
    c. Same as a, $\rightarrow (E_1E_mE_1)(L_vL_d)U_2U_1I$, increase of U up to U_{10}, bifurcation of individual lobes ..... Pronoritidae
11. Same as 10c, but L_v becomes part of the external saddle, which becomes incised (Fig. 12,*g*) ..... Medlicottiaceae
12. $*ELI(?) \rightarrow E_mE_xLU_yU_1I$ [$E_x{=}E_{i-1}$, $U_y{=}U_{2-11}$] ..... Sageceratacea

II. Order Clymeniida

13. $ELI, \rightarrow ELUI, \rightarrow EA_2A_1LU_1U_2I$ (Fig. 12,*i*)
    or$\rightarrow (E_1E_mE_1)LU_2U_1I$ ..... Gonioclymeniaceae
14. $*ELI \rightarrow (E_1E_1)L(I_1I_1), \rightarrow L$ ..... Parawocklumeriaceae
15. $*ELI \rightarrow LI, \rightarrow ALI$, or LUI, or $ALUI$ (Fig. 12,*k*) ..... Clymeniaceae

III. Order Phylloceratida

16. Otoceratacea
    a. $*ELI? \rightarrow ELU_2{:}U_1I_1$ (Fig. 13,*a*) ..... Xenodiscidae
    b. $*ELU_1I \rightarrow ELU_2U_3{:}U_1I_1$ (Fig. 13,*b*) ..... Ophiceratidae
    c. $*ELU_1I \rightarrow ELU_2U_3U_5{:}U_1U_1I_1$ (Fig. 13,*c*) ..... Otoceratidae

17. Phylloceratacea
    a *$ELU_1I \rightarrow ELU_2U_3{:}U_1I_l$ (or $ELU_2U_{1v}{:}U_{1d}I_l$ and therefore may be included in Meekoceratacea) Ussuritidae,
    (Fig. 13,*d*)$\rightarrow ELU_2U_3U_5U_6{:}U_4U_1I_l(?)$ ..... "Palaeophyllitidae"
    b. *$ELU_1I?$ and *$ELU_2U_1I \rightarrow ELU_2U_3U_1I_l \rightarrow$ $ELU_2(U_3{=}S)U_1I_l \rightarrow ELU_2(U_3{=}S)U_1I$ (*I* frilled) ..... Discophyllitidae
    c. *$ELU_2U_1I \rightarrow ELU_2(U_3{=}S)U_1I_l \rightarrow$ $ELU_2U_3(U_4{=}S)U_1I_l$ (Fig. 5, 15,*a*) ..... Phylloceratidae
18. Meekoceratacea
    *$ELU_1I \rightarrow ELU_2{:}U_1I_l \rightarrow ELU_2U_3{:}U_1I_l$
19. Clydonitacea
    a. *$ELU_1I \rightarrow ELU_2{:}U_1I \rightarrow ELU_2U_3{:}U_1I$ (Fig. 13,*f*) ..... Clydonitidae, Clionitidae, Arpaditidae, Tibetitidae, Thisbitidae, Trachyceratidae
    b. *$ELU_1I \rightarrow ELU_2U_1{:}I$ (*I* single-pointed) ..... Lecanitidae, Nannitidae
    c. *$ELUI \rightarrow ELU{:}I$ (*I* single-pointed) (Fig. 13,*g*) ..... Choristoceratidae
20. Tropitacea
    *$ELU_1I \rightarrow ELU_2{:}U_1I$
21. Ceratitacea
    a. *$ELU_1I \rightarrow ELU_2U_3{:}U_1I_l \rightarrow ELU_2U_3U_5U_7{:}U_6U_4U_1I_l$ (Fig. 13,*h*) ... Ceratitidae
    b. *$ELU_1I \rightarrow ELU_2U_4U_6U_8U_{10}U_{11}U_9U_7U_5U_3U_1I_l$ (Fig. 14,*a*) ..... Hungaritidae
    c. *$ELU_1I \rightarrow ELU_2U_4{:}U_3U_1I_l$ ..... Aplococeratidae
    d. *$ELU_1I \rightarrow ELU_2(U_{1v}{:}U_{1d})I_l$ ..... Prionitidae
22. Dinaritacea
    *$ELU_1I \rightarrow EL(U_{1v}{:}U_{1d})I_l$ (Fig. 13,*i*)
23. Lobitacea
    *$ELU_1I \rightarrow E(L_vL_d)(U_{2v}U_{2d})U_3{:}U_{1v}U_{1d}I_l$ (Fig. 14,*b*)
24. Arcestacea
    ?a. *$ELU_1I \rightarrow ELU_2(U_3{=}S)U_1I_l$ (Fig. 13,*k*) ..... Procarnitidae
    b. *$ELU_1I \rightarrow ELU_2(U_3{=}S)U_1I_l$ (Fig. 14,*c*) ..... Megaphyllitidae
    c. *$ELU_2U_1I \rightarrow EALU_2U_3U_1U_{nv}U_{nd}I$ (Fig. 14,*d*) ..... Arcestidae
25. Ptychitacea
    *$ELU_1I \rightarrow ELU_2(U_3{=}S)U_1I$ (Fig. 14,*e*)
26. Pinacoceratacea
    Suture unknown

IV. Order Lytoceratida
    Suborder Lytoceratina
27. Lytoceratacea
    a. *$ELU_1I(?) \rightarrow ELU_2(U_{1v}{:}U_{1d})I$ (Fig. 14,*f*) ..... Trachyphyllitidae
    b. *$ELU_2U_1I \rightarrow ELU_2(U_{1v}{:}U_{1d})I_s$ (Fig. 6, 14,*g*)$\rightarrow$ $ELU_2U_3{:}(U_{1v}U_{1d})I_s$ ..... Lytoceratidae
    c. *$ELU_2U_1I \rightarrow ELU_2U_1I_s$ ..... Ectocentritidae
28. Tetragonitacea
    a. *$ELU_2U_1I \rightarrow ELU_2U_1I_s$ (U_1 suspensive) (Fig. 14,*h*) ..... Gaudryceratidae
    b. *ELU_2U_1I and $ELU_2U_3U_1I \rightarrow$ $ELU_2U_3(U_4{=}S)U_1I_s$ (Fig. 14,*i*) ..... Tetragonitidae
    Suborder Ammonitina
29. Psiloceratacea
    a. *$ELU_2U_1I \rightarrow ELU_2U_3{:}U_{1v}U_{1d}I$ (up to $U_4{=}S$) (Fig. 15,*b*) ..... Psiloceratidae,

Schlotheimiidae,
Arietitidae (p.p.),
Polymorphitidae,
Amaltheidae,
Dactylioceratidae

b. $*ELU_2U_1I \rightarrow ELU_2U_3U_{1v}:U_{1dv}U_{1dd}I \rightarrow ELU_2U_3:U_{1v}U_{1d}I$ (Fig. 15,*c*) ..... Eoderoceratidae

c. $ELU_2(U_{1v}=S)U_{1d}I$ ..... Cymbitidae, Liparoceratidae

d. $*ELU_2U_1I \rightarrow ELU_2U_3:U_1I \rightarrow ELU_2:U_1I$ (Fig. 15,*d*) ..... Arietitidae (p.p.), Echioceratidae, Oxynoticeratidae, Phricodoceratidae, Aegoceratidae

30. Hildoceratacеae

$*ELU_2U_1I \rightarrow ELU_2U_3:U_1I \rightarrow ELU_2U_3U_5U_7U_9U_{11}U_{12}:U_{10}U_8U_6U_4U_1I$ (Fig. 15,*e*)

31. Hammatoceratacеae

a. $*ELU_2U_1I \rightarrow ELU_2U_3U_4:(U_{1v}U_{1d})I$ (Fig. 15,*f*) ..... Hammatoceratinae

b. $*ELU_2U_1I \rightarrow ELU_2U_3U_1I$ ..... Phymatoceratinae

c. ? $ELU_2U_1:I$ (Fig. 15,*h*) ..... Tmetoceratidae

d. $*ELU_2U_1I \rightarrow ELU_2U_3U_4:U_1I$ ..... Dumortieriidae

e. $*ELU_2U_1I \rightarrow ELU_2U_3U_4U_5U_7U_8U_6U_{1v}U_{1d}I$ (to U_{13}) (Fig. 15,*g*) ..... Oppeliinae

f. $*ELU_2U_1I \rightarrow ELU_2U_3:U_{1v}U_{1d}I$ ..... Phlycticeratinae

g. $*ELUI \rightarrow ELU_2U_5:U_4U_3U_{1v}U_{1d}I$ ..... Paroniceratidae

32. Haploceratacеae

a. $*ELU_2U_1I \rightarrow ELU_2U_3U_5:U_6U_4U_1I$ ..... Graphoceratidae, Strigoceratidae

b. $*ELU_2U_1I \rightarrow ELU_2U_3U_5U_4U_1I \rightarrow ELU_2U_3U_5U_7U_9U_{11}U_{10}U_8U_6U_4U_1I$ (Fig. 15,*i*) ..... Sonniniidae

c. $*ELU_2U_1I \rightarrow ELU_2U_3U_5U_7U_8:U_6U_4U_1I$ (Fig. 15,*k*) ..... Haploceratidae

d. $*ELU_2U_1I \rightarrow ELU_2U_3U_5:U_6U_4U_1I$ ..... Mazapilitinae

e. $*ELU_2U_1I \rightarrow ELU_2U_3U_5U_7U_9:U_8U_6U_4U_1I$ ..... Aconeceratinae

33. Stephanoceratacеae

a. $*ELU_2U_1I \rightarrow ELU_2U_3:(U_{1v}U_{1d})U_nI$ (Fig. 8, 16,*a*) $\rightarrow ELU_2U_3U_5:U_4U_1U_nI$ ..... Otoitidae

b. $*ELU_2U_1I \rightarrow ELU_2U_3U_5:U_4U_1U_nI$ (Fig. 16,*b*) ..... Stephanoceratidae, Sphaeroceratidae

c. $*ELU_2U_1I \rightarrow ELU_2U_3U_4:U_5U_1U_nI$ ..... Macrocephalitidae

d. $*ELU_2U_1I \rightarrow ELU_2U_3:U_1U_nI$ ..... Kosmoceratidae

e. $*ELU_2U_1I \rightarrow ELU_2U_3U_4U_1U_nI$ ..... Cardioceratidae

f. $*ELU_2U_1I \rightarrow ELU_2U_3U_5:U_4U_1U_nI$ (Fig. 16,*e*) ..... Morphoceratidae, Parkinsoniidae

g. $*ELU_2U_1I \rightarrow EU_2I$ (Fig. 16,*f*) or ELU_2I ..... Spiroceratidae, Acuariceratidae

h. $*ELU_2U_1I \rightarrow ELU_2(U_3=S)U_1I$ (Fig. 16,*c*) ..... Tulitidae

i. $*ELU_2U_1I \rightarrow ELU_2:U_3U_1I$ (Fig. 16,*d*) ..... Pachyceratidae

k. $*ELU_2U_1I \rightarrow ELU_2U_3U_4:U_1I$ ..... "Oecoptychiidae"

34. Perisphinctacеae

a. $*ELU_2U_1I \rightarrow ELU_2U_3(U_4=S)U_{1v}U_{1d}I$ (Fig. 16,*g*) ..... Perisphinctidae, Berriasellidae, Reineckeiidae,

b. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$*U*$_4$*U*$_1$*I* (to *U*$_7$) (Fig. 16,*h*) ..... Craspeditidae, Olcostephanidae, Oosterellidae, Endemoceratidae, Aspidoceratidae

c. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$:*U*$_1$*I* ..... Peltoceratidae

d. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$:*U*$_{1v}$*U*$_{1d}$*I* ..... Simoceratidae

e. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$(*U*$_3$=*S*)*U*$_1$*I*→ *ELU*$_2$*U*$_3$(*U*$_4$=*S*)*U*$_{1v}$*U*$_{1d}$*I*→*ELU*$_2$(*U*$_3$=*S*)*U*$_1$*I* ..... Holcodiscidae

35. Hoplitaceae

a. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$*U*$_5$*U*$_7$:*U*$_6$*U*$_4$*U*$_1$*I* (Fig. 16,*i*) ..... Eodesmoceratidae

b. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$*U*$_5$*U*$_7$:*U*$_8$*U*$_6$*U*$_4$*U*$_1$*I* ..... Pulchelliidae

c. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$(*U*$_4$=*S*)*U*$_{1v}$*U*$_{1d}$*I* (Fig. 16,*k*) ..... Desmoceratidae, Kossmaticeratidae, Pachydiscidae, Hoplitidae, Schloenbachiidae, Placenticeratidae (with trifurcation in *L*)

d. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$*U*$_4$*U*$_{1v}$*U*$_{1d}$*I* ..... Silesitidae, Leymeriellidae

36. Acanthocerataceae

a. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$*U*$_5$:*U*$_6$*U*$_4$*U*$_1$*I* (Fig. 16,*l*) ..... Brancoceratidae, Lyelliceratidae

b. without *U*$_6$ ..... Acanthoceratidae, Vascoceratidae

c. **ELU*$_2$*U*$_1$*I*→*ELU*$_2$*U*$_3$*U*$_1$*I* ..... Collignoniceratidae

d. **ELU*$_2$*U*$_1$*I*→*EALU*$_2$*U*$_3$*U*$_5$*U*$_7$*U*$_9$*U*$_{11}$:*U*$_{10}$*U*$_8$*U*$_6$*U*$_4$*U*$_1$*I* ..... Sphenodiscidae

Suborder Ancyloceratina

37. Ancyloceratacea

**ELUI*→*ELUI* (Fig. 9,*1*)

38. Scaphitaceae

**ELUI*→*ELUI*→*ELp*$_1$*p*$_2$*p*$_3$:*U*$_v$*U*$_d$*I* (Fig. 9,*2*)

39. Douvilleiceratacea

a. **ELUI*→*ELUI*→*EL*$_v$*L*$_d$*U*$_v$:*U*$_d$*I* (Fig. 9,*3*) ..... Douvilleiceratidae

b. **ELUI*→*EL*$_v$*L*$_d$*UI* ..... Astiericeratidae

c. **ELUI*→*ELU*$_v$:*U*$_d$*I* (Fig. 10) or *ELU*$_{vv}$*U*$_{vd}$:*U*$_d$*I* ..... Parahoplitidae

d. **ELUI*→*ELUI* ..... Trochleiceratidae

40. Deshayesitaceae

**ELU*$_2$*?I*→*ELU*$_2$*?U*$_3$*?*:*U*$_1$*?I* (Fig. 9,*4*)

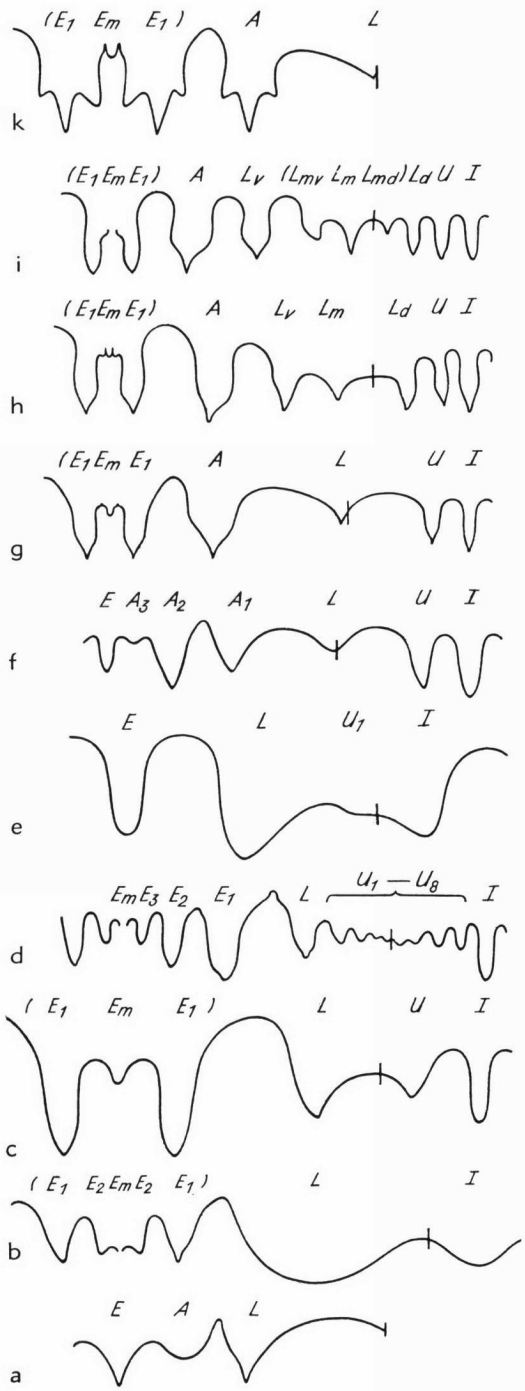

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FIG. 11. Adult sutures of Paleozoic Anarcestina and Goniatitina.

a. Maenioceras terebratum (SANDBERGER), Middle Devonian (Givetian), Germany (from Bogoslovskiy, *et al.,* 1962, after Holzapfel, 1895).

b. Augurites mirandus BOGOSLOVSKIY, Middle Devonian (Eifelian), USSR (from Bogoslovskiy, 1961).

c. Manticoceras sinuosum (HALL), Upper Devonian (Frasnian), USA (from Miller & Furnish, 1957, after Clarke, 1899).

d. Mesobeloceras thomasi GLENISTER, Upper Devonian (Frasnian), Australia (from Bogoslovskiy, *et al.,* 1962, after Glenister, 1958).

e. Clymenoceras insolitum SCHINDEWOLF, Upper Devonian (Famennian), Germany (from Bogoslovskiy, *et al.,* 1962, after Schindewolf, 1938).

f. Discoclymenia cucullata (VON BUCH), Upper Devonian (Famennian), Germany (from Schindewolf, 1951).

g. Goniatites choctawensis SHUMARD, Mississippian, USA (from Miller & Furnish, 1957).

h. Eothinites kargalensis kargalensis RUZHENTSEV, Lower Permian (Artinskian), USSR (from Ruzhentsev, 1956).

i. Pseudoschistoceras simile TEICHERT, Lower Permian, Australia (from Bogoslovskiy, *et al.,* 1962, after Teichert, 1944).

k. Delepinoceras bressoni cantabricus KULLMANN, Upper Carboniferous (lower Namurian), Spain (from Kullmann, 1962).

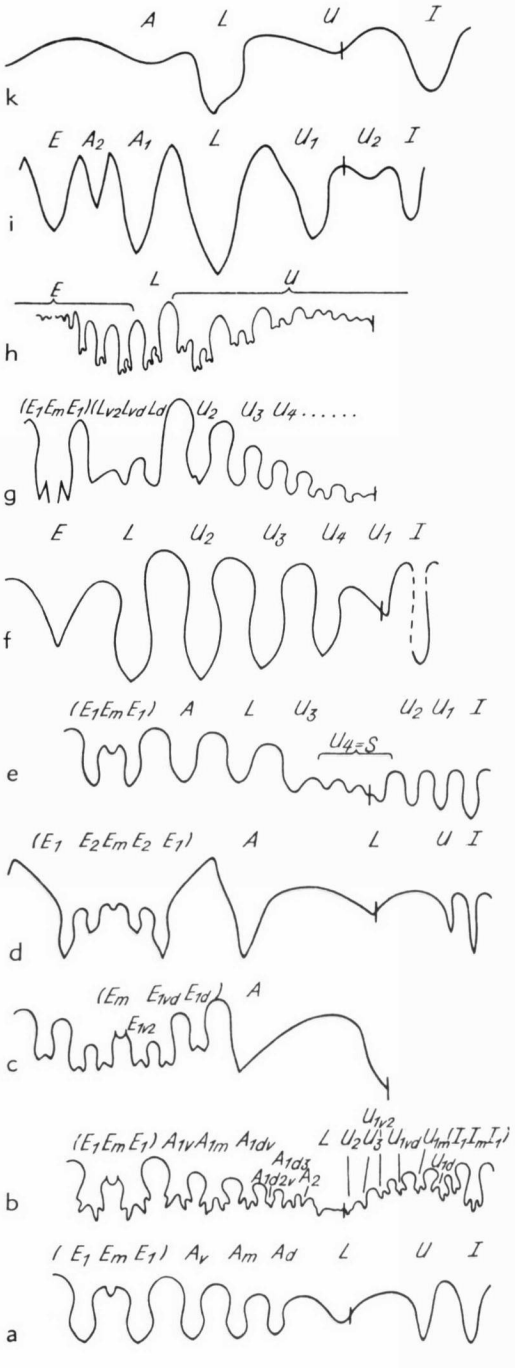

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Fig. 12. Adult sutures of Paleozoic Goniatitina, Prolecanitina and Clymeniida.

a. Agathiceras uralicum Karpinskiy, Lower Permian (Artinskian), USSR (from Miller & Furnish, 1957).

b. Popanoceras sobolewskyanum (de Verneuil), Lower Permian (Artinskian), USSR (from Ruzhentsev, 1956).

c. Asturoceras subdivisum (Kullmann), Upper Carboniferous (lower Namurian), Spain (from Kullmann, 1962).

d. Neodimorphoceras texanum (Smith); Upper Pennsylvanian, USA (from Bogoslovskiy, *et al.,* 1962, after Miller & Downs, 1950).

e. Crimites subkrotowi Ruzhentsev, Lower Permian (Artinskian), USSR (from Ruzhentsev, 1956).

f. Prolecanites (Cantabricanites) postapplanatus Kullmann, Lower Carboniferous (upper Visean), Spain (from Kullmann, 1963).

g. Prouddenites primus Miller, Upper Pennsylvanian, USA (from Miller & Furnish, 1957).

h. Pseudosageceras multilobatum Noetling, Lower Triassic, USSR (from Bogoslovskiy, *et al.,* 1962, after Kiparisova, 1947).

i. Sphenoclymenia maxima (Münster), Upper Devonian (Famennian), Germany (from Schindewolf, 1957).

k. Cymaclymenia striata (Münster), Upper Devonian (Famennian), Germany (from Schindewolf, 1957).

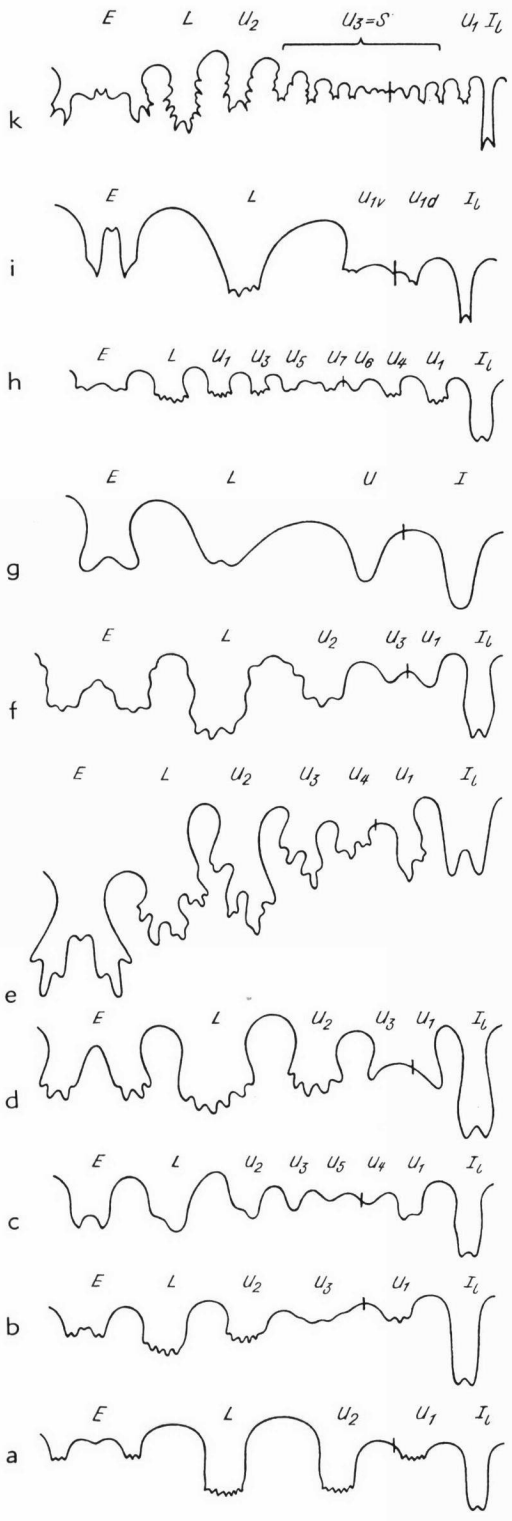

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FIG. 13. Phylloceratid adult sutures of the Upper Permian and Triassic.

a. Xenodiscus sp., Upper Permian, Salt Range.
b. Ophiceras sakuntala DIENER, Lower Triassic (lower Scythian), Himalayas.
c. Otoceras sp. cf. *O. woodwardi* GRIESBACH, Lower Triassic (lower Scythian), Himalayas.
d. Leiophyllites taramellii (MARTELLI), Middle Triassic (Anisian), Bosnia.
e. Monophyllites sphaerophyllus (HAUER), Middle Triassic (Anisian), northern Alps.
f. Trachyceras sp. cf. *busiris* (MÜNSTER), Upper Triassic (lower Carnian), Tyrol.
g. Choristoceras marshi (HAUER), Upper Triasstic (Rhaetian), northern Alps.
h. Ceratites nodosus (BRUGUIÈRE), Middle Triassic, Germany.
i. Dinarites asiaticus SHEVYREV, Lower Triassic (upper Scythian), USSR.
k. Procarnites kokeni (ARTHABER), Lower Triassic (upper Scythian), USSR.
(*a-f,h* from Schindewolf, 1968; *g* from Wiedmann, 1969b; *i,k* from Shevyrev, 1968.)

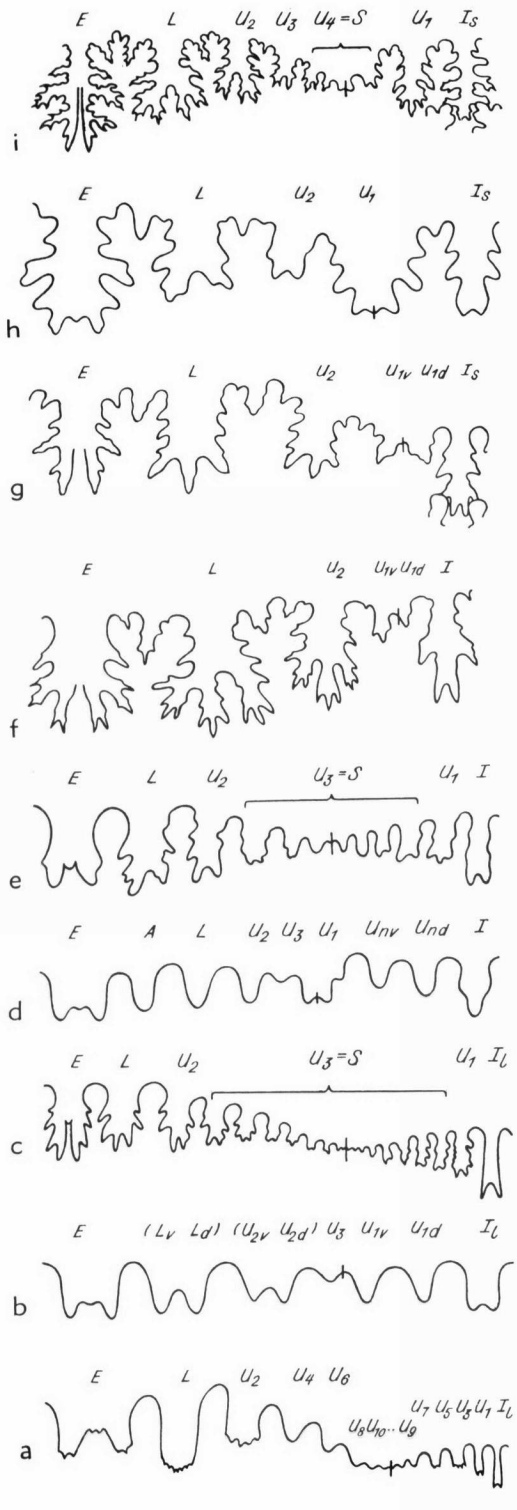

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Fig. 14. Adult sutures of Triassic Phylloceratida and Triassic-Cretaceous Lytoceratina.

a. Longobardites caucasicus (Shevyrev), Middle Triassic (upper Anisian), USSR.

b. Paralobites nautilinus (Münster), Upper Triassic (lower Carnian), Tyrol.

c. Megaphyllites prometheus Shevyrev, Middle Triassic (upper Anisian), USSR.

d. Arcestes bicarinatus (Münster), Upper Triassic (lower Carnian), Tyrol.

e. Sturia sansovinii (Mojsisovics), Middle Triassic (Anisian), USSR.

f. Trachyphyllites costatus Arthaber, Upper Triassic (Norian), Timor.

g. Derolytoceras tortum (Quenstedt), Lower Jurassic (upper Pliensbachian), Germany.

h. Gaudryceras tenuiliratum Yabe, Upper Cretaceous (Senonian), Hokkaido.

i. Tetragonites subbeticus Wiedmann, Lower Cretaceous (upper Aptian), Balearics.

(*a,c,e* from Shevyrev, 1968; *b,d,h* from Schindewolf, 1968; *f,g* from Wiedmann, 1969b; *i* from Wiedmann, 1962c.)

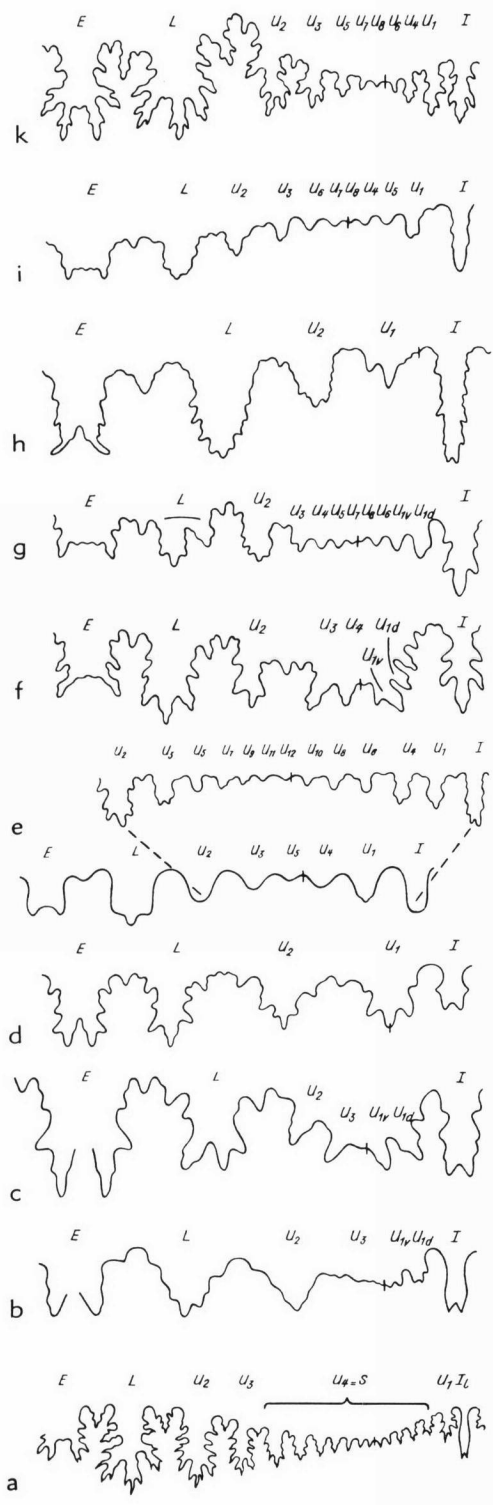

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FIG. 15. Adult sutures of Jurassic-Cretaceous Phylloceratina and Ammonitina.

a. Phylloceras onoense (STANTON), Lower Cretaceous (Aptian), USA.
b. Psiloceras psilonotum (QUENSTEDT), Lower Cretaceous (lower Hettangian), Germany.
c. Eoderoceras armatum (SOWERBY), Lower Jurassic (upper Sinemurian), England.
d. Phricodoceras taylori (J. DE C. SOWERBY), Lower Jurassic (lower Pliensbachian), Germany.
e. Pseudolioceras compactile (SIMPSON), Lower Jurassic (upper Toarcian), Germany.
f. Hammatoceras insigne (ZIETEN), Lower Jurassic (upper Toarcian), France.
g. Paroecotraustes tenuistriatus (GROSSOUVRE), Middle Jurassic (upper Bathonian), Germany.
h. Tmetoceras scissum (BENECKE), Middle Jurassic (lower Bajocian), Italy.
i. Dorsetensia sp., Middle Jurassic (middle Bajocian), Germany.
k. Haploceras grasianum (D'ORBIGNY), Lower Cretaceous (lower Valanginian), France.

(*a* from Wiedmann, 1962b, *b* from Wiedmann, 1969b; *c,d* from Schindewolf, 1962; *e-i* from Schindewolf, 1964; *k* from Wiedmann, 1966a.)

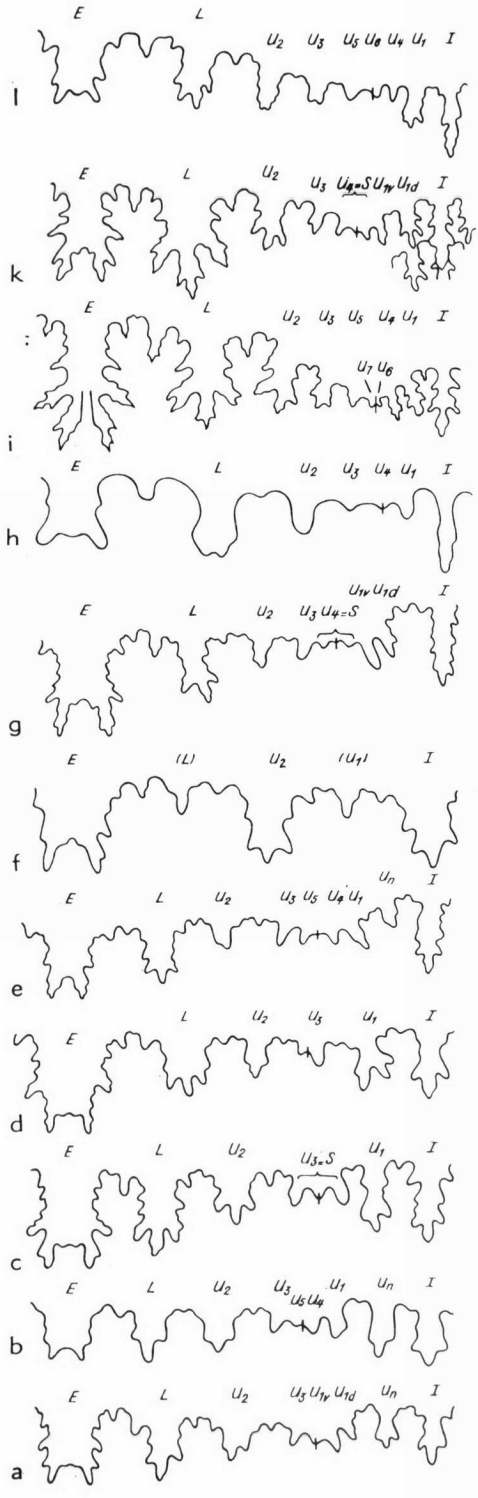

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FIG. 16. Adult sutures of Jurassic-Cretaceous Ammonitina.

a. Otoites sp. cf. *O. tumulosus* WESTERMANN, Middle Jurassic (middle Bajocian), England.

b. Chondroceras tenue WESTERMANN, Middle Jurassic (middle Bajocian), Germany.

c. Bullatimorphites sp. cf. *B. microstoma uhligi* (POPOVICI-HATZEG), Middle Jurassic (upper Bathonian), Germany.

d. Pachyceras lalandeanum (D'ORBIGNY), Upper Jurassic (lower Oxfordian), France.

e. Parkinsonia sp. cf. *P. parkinsoni* (SOWERBY), Middle Jurassic (upper Bajocian), Germany.

f. Spiroceras bifurcati (QUENSTEDT), Middle Jurassic (upper Bajocian), Germany.

g. Grossouvria sulcifera (OPPEL), Upper Jurassic (Callovian), Germany.

h. Oosterella stevenini (NICKLÈS), Lower Cretaceous (upper Valanginian), Spain.

i. Eodesmoceras celestini (PICTET & CAMPICHE), Lower Cretaceous (Valanginian), Switzerland.

k. Neosilesites balearensis (FALLOT), Lower Cretaceous (upper Aptian), Balearics.

l. Lyelliceras lyelli (LEYMERIE in D'ORBIGNY), Lower Cretaceous (middle Albian), France.

(*a-e* from Schindewolf, 1965; *f* from Schindewolf, 1961; *g* from Schindewolf, 1966; *h,i* from Wiedmann, 1966a; *k,l* from Wiedmann, 1966b.)

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